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CONTRIBUTIONS TO THE STUDY OF THE
TRYPETHELIACEAE¹

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INTRODUCTION

An interesting anomaly exists between the prevailing ideas as to the relationships of the species of pyrenocarpous lichens with similar species of pyrenomycetous fungi. Although few lichenologists have studied related fungi to any extent, most of them are firmly convinced that the Pyrenocarpeae are monophyletic in origin and that the so-called "lichen symbiosis" has been an association of considerable age that has resulted in significant evolutionary modifications within the group. The majority of mycologists, on the other hand, although as unacquainted with the details of lichen morphology as are the lichenologists with those of the fungi, are as firmly convinced that the same lichens are predominantly the result of the parasitism of various algae by different species of fungi and correspondingly that the group is not a phylogenetically distinct unit.

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A preliminary survey of the families of pyrenocarpous lichens indicated that a study of the Trypetheliaceae should help to clarify the issue outlined above as well as increase our knowledge of the detailed morphology of lichens. This family is almost universally recognized by lichen systematists and they have differentiated it from other families chiefly in that "the perithecia are borne embedded in a stroma." The members of the family are often compared with the stromoid pyrenomyces where similar structures are said to exist, and the greatest argument among lichenologists for the retention of the Trypetheliaceae as a family has been the major role that the stroma plays in the classification of the group considered analogous to it in the fungi. This latter fact suggested that one logical approach to the study of the relation of lichens to the fungi would be to examine the manner of development of the Trypetheliaceae and to compare this with that of the stromoid members of the Pyrenomyces. Such an investigation, which has not hitherto been attempted, is reported in this paper. The results obtained do not fulfill all the predictions of those who have failed to base their observations upon developmental studies, and contributions are recorded to the detailed development of members of the Trypetheliaceae, their microscopic morphology in relation to their taxonomic treatment, and their probable evolutionary development.

HISTORICAL REVIEW

The Trypetheliaceae is a relatively ancient lichen family, its demarcation from other groups being suggested by Eschweiler as early as 1824. Tuckerman (1872), Müller-Argau (1885), Zahlbruckner ('03-'07, '26), Smith ('21), Malme ('24), Fink ('35), and Keissler ('37) are systematists whose similar treatment indicates its almost universal acceptance. In its earlier stages the family included genera now assigned to other families, as *Arthonia*, *Glyphis*, *Chiodecton*, and *Astrothelium*. Müller-Argau, in 1885, delimited it to its generally accepted present form, embracing the genera *Melanotheca*, *Trypethelium*, *Tomasellia*, *Laurera*, and *Bottaria*. Since that time the

Trypetheliaceae have been considered as differentiated from other lichens by the following combination of characters: asci borne enclosed in a flask-shaped fruiting body (perithecium); perithecia united in a "stroma," each perithecium erect, with its own apical pore; thallus crustose, containing *Trentepohlia*. Only two lichenologists, Wainio (1890) and Watson ('29), have distributed such lichens among other genera or families.

A glance at the other families of the Pyrenocarpeae immediately shows that the chief characteristic of the Trypetheliaceae is the aggregation of separate perithecia into a so-called stroma. It is an interesting fact that the microscopic structure of this fundamental character of the family has never been accurately described. This is all the more striking when one carefully considers the following statement which was attached by Wainio (1890, footnote p. xxiii) to a discussion of the stromatic appearance of *Glyphis*, *Chiodecton*, and *Trypethelium*: "Pour les distinguer des stromes des Champignons, nous nommons *pseudostromes* les excipula adhérents, parce que ces organes, aussi bien par leur structure que par leur mode de développement, présentent des différences importantes." Wainio did not describe in detail the major differences that he insinuates are visible between the stromata of fungi and the structures present in the lichens cited. It is evident from the discussion in the text, however, that his concept of pseudo-stromata was somewhat loosely formulated or else was based upon macroscopic resemblances for he considered that not only species at present assigned to the Trypetheliaceae but that *Glyphis* and *Pertusaria*, among others, possessed them. The term is perpetuated in the literature in connection with several families of lichens (Trypetheliaceae, Astrotheliaceae, Mycoporaceae, Thelotremaeae) by Miss Smith ('21), but she merely accepted Wainio's statements as authority for doing so and did not describe the morphological details of the structure she designated in such a manner.

In discussing the Trypetheliaceae in the first edition of Engler-Prantl's 'Die natürlichen Pflanzenfamilien,' Zahlbrückner ('03, p. 69) made the following statements:

Wainio anerkennt das Stroma oder "Pseudostroma," wie er es bezeichnet, nicht als generisches Merkmal und betrachtet demgemäß die Gattungen der *Trypetheliaceae* als Untergattungen der analogen Genera der *Pyrenulaceae*. Zweifellos sind intermediäre Formen zwischen den genannten beiden Familien vorhanden, und sie sind in ähnlicher Weise durch Übergänge verbunden wie die *Lecanoraceae* mit den *Leiodeaceae*. Bei dem durch den polyphyletischen Ursprung bedingten Parallelismus der Flechtengattungen und bei dem Umstand, dass die Entwicklungsgeschichte der Stromen noch nicht festgestellt ist, scheint er derzeit angezeigt zu sein, die stromabildenden Flechtengenera als eigene Familie zu behandeln.

The same remarks were repeated without alteration in his treatment of the family in the second edition of the same work (Zahlbrückner, '26, pp. 81-82), and in addition the following significant sentence was added at the end: "Diesen Vorgang befolgen auch die Mykologen."

The most recent treatment of the family is that of Keissler ('37), who stated in this connection (p. 422):

Das Characteristische für die vorliegende Familie ist die Ausbildung eines Stromas. Dieses Merkmal spielt bekanntlich in der Mykologie bei den Pyrenomyceeten für die Abgrenzung der Gruppen eine grosse Rolle. Es scheint daher wohl angezeigt, jene Gattungen der Flechten, welche sich durch ein solches Stroma auszeichnen, zu vereinigen und als eigene Familie abzutrennen. Anderer Meinung ist Vainio, der nur von einem Pseudostroma spricht, dessen Vorhandensein er nicht einmal als generisches Merkmal wertet, sondern die Gattungen der Trypetheliaceen als Subgenera der analogen Gattungen bei den Pyrenulaceen betrachtet. Dementsprechend fasst er zum Beispiel *Melanotheca* als Subgenus von *Pyrenula* auf. Es lässt sich ja nicht leugnen, dass intermediäre Formen zwischen beiden Familien vorkommen. Es scheint aber doch, solange man über die Entwicklung des Stromas bei den Flechten noch nichts Genaues weiß, angezeigt, dem Beispiele der Mykologen in bezug auf die Wertung des Stromas zu folgen und die Trypetheliaceen als eigene Familie aufzufassen.

The existing lack of knowledge with reference to the detailed development of the Trypetheliaceae has resulted in the present paper. It is evident that special emphasis should be placed on the hitherto unknown morphology of the so-called stroma.

MATERIALS AND METHODS

The author has had at his disposal during the course of the investigation numerous collections of pyrenocarpous lichens and some material killed and fixed in the field in Costa Rica by

Dr. C. W. Dodge during the summer of 1936. This has been supplemented by personal collections made near Lake Pontchartrain, Louisiana, in the spring of 1937, and in several states bordering the Gulf of Mexico (particularly Mississippi and Florida²) during December, 1938, and January, 1939.

Material killed and fixed in the field was subsequently embedded in paraffin (through the butyl-alcohol dehydration series recommended by Zirkle, '30) or in low-viscosity nitrocelulose (Koneff and Lyons, '37); microtome sections were cut; the resulting sections were stained and mounted in balsam. Sections 7-10 μ in thickness usually proved most useful for observation, and Heidenhain's iron-alum haemotoxylin with a counterstain of phloxine, the best staining combination. The slides resulting form the basis of the morphological observations described below.

MORPHOLOGY AND DEVELOPMENT

The thallus of the Trypeteliaceae is very simple. It can be divided into three layers which may be designated as: (1) cortex, (2) gonidial layer, and (3) medulla—following the terminology applied in other groups of lichens (pl. 4, fig. 4). The cortex of most members of the family is very poorly developed, consisting merely of those strands of hyphae intermingled with the bark cells that are located above the algal zone. Some lichenologists might object to calling the structure a cortex, but it is homologous with that structure and for practical purposes must be considered a primitive one. In some members of the family an amorphous crust is formed over the tissue which covers the algal zone. The width of the tissue here designated as cortical varies with the species, and it is convenient to have a term for it that will be useful for taxonomic reference. The gonidial layer is usually fairly thin, somewhat poorly developed, and at times even seems unconnected with the fruiting body of the lichen. The medulla con-

²The author wishes to acknowledge assistance offered in the field by Dr. T. W. Brasfield and Mr. Severin Rapp, at Perkinston, Mississippi, and Sanford, Florida, respectively, during this trip.

sists of threads of hyphae intermingled with the bark cells that are located on the inside of the gonidial layer.

In this section the life history of *Melanotheca aggregata* will be described. For other organisms only such points will be noted as are so similar to or so divergent from the processes in *M. aggregata* as to deserve especial comment. Microscopic measurements peculiar to the species are not often given, except that the thickness of the cortex and gonidial layer is usually recorded. The latter structures are "lichen characters" formed by the association of the fungus and the alga. The degree of their development seems as indicative of the age of the association as the morphology of the "stroma," to which the greatest attention is naturally directed.

MELANOThECA

Melanotheca aggregata (Fée) Müll. Arg.—

It is convenient to begin the description of the development of this species with the germination of the ascospore. This spore swells slightly and a germ-tube is usually sent out from one or both of the terminal cells; the central cells, however, frequently sprout also. Germination has been induced in various nutrient solutions and on bark. Growth is not vigorous with any of these but is relatively more so on bark where the germ-tubes penetrate the surface and form a mycelial network between the cells. The network has reached a considerable size with algae absent.

Filaments of *Trentepohlia* are able to penetrate the bark of many trees and they may live as far as eight to ten cell layers below the surface. It makes little difference whether the alga or the fungus inhabits a particular area first. After they come in contact a distinct vegetative thallus is formed through their combined growth.

The thallus of *Melanotheca aggregata* is completely embedded in the periderm. The fungal component consists of very slender, densely interwoven, hyaline hyphae which show few septa. The youngest stages in the formation of the peritheciun consist merely of small spherical clumps of hyphae

located on either side of the gonidial layer some distance below the surface of the bark (pl. 2, fig. 1). The primordia may become as large as 12μ in diameter before visible differentiation takes place.

Darkening of the bark above the perithecial primordium usually accompanies its earliest stages. The darkened area grows wider and deeper throughout the subsequent growth of the perithecium and pseudostroma as will be noted below.

The outer hyphae of the spherical mass assume a definite polarity, growing toward the point which later becomes the apex of the perithecium, and the mass becomes more or less ovoid. The bark cells become more carbonaceous during this process, and it seems fairly evident that the fungal hyphae are the primary influences altering these cells. The ascogonia are now delimited, several being produced in each perithecium (pl. 2, fig. 2). Each ascogonium is composed of a spiral or coiled series of uninucleate cells.

The tissue surrounding the ascogonia continues to alter the bark cells, and these changes, combined with the pressure formed by the ever-increasing mass of hyphae, give rise to the perithecial cavity. Expansion continues until the tip of the mass reaches the exterior of the bark and an ostiole is formed. Trichogynes sent out from the ascogonia grow upward and project in tufts through the ostiole (pl. 2, fig. 3). In all cases favorable for examination they appear to be composed of uninucleate cells. Though they usually extend barely beyond the surface they have been recorded as reaching a distance of 30μ above the bark.

It should be emphasized that the perithecial cavity has been delimited before great differentiation of the ascogonia has taken place and that its actual formation is due directly to the altering of the bark cells and the pressure exerted on these cells by vegetative hyphae. It should also be noted that the ostiole is formed by the action of these same hyphae before the formation of the trichogynes (and if fusion of spermatia and trichogynes occurs, before any ascogenous hyphae have been formed).

Spermagonia (pycnidia) become evident at this time. They are exceptionally small in the material examined, being about 10-30 μ in diameter. Each spermagonium (pycnidium) contains numerous minute spermatia (pycnidiospores). Although these structures appear regularly enough to suggest that they are a component part of the lichen it is also possible that they might represent a parasitic or saprophytic imperfect fungus.

No cytological evidence for the fusion of spermatia with the trichogynes has been observed. The trichogynes disappear rapidly and the ascogonia enlarge, becoming multinucleate. Several of the ascogonia give rise to ascogenous hyphae, and at least four to eight (sometimes more) can be readily identified within each perithecium. Branches given off by the ascogonia result in the formation of a concave layer at the base of the perithecium (pl. 2, fig. 4). At the same time the perithecium and the perithecial cavity increase in size, primarily through the influence of the hyphae of the envelope upon the surrounding bark cells. Many of these cells lose their normal appearance, shrink, and become hard and carbonaceous. Others are probably digested as the perithecial envelope and its contents expand. Some, particularly those in the uppermost two or three cell layers, are probably sloughed off.

It is common for several perithecia to arise in the same vicinity and to develop simultaneously. Each perithecium, however, originates deep within the substrate and develops independently below the surface of the bark (pl. 2, fig. 7). At the stage described to this point a stroma has not been formed and there is no indication that one will be. Each perithecium is bounded by a definite carbonaceous wall, although the bark cells above it have also become dark and carbonaceous and frequently extend a short distance from the cavity. The bark cells are in close relation with and are often completely surrounded by vegetative hyphae of the fungal component of the lichen. The so-called stroma then originates by the expansion of this carbonaceous tissue so as to include the walls of several adjacent perithecia (pl. 2, fig. 5). Individuals of this species produce perithecia in such great abundance that prac-

tically all eventually become embedded in this tissue by virtue of their proximity to each other. The "stroma" which develops in this organism is obviously composed primarily of bark cells and differs materially from stromata as ordinarily conceived in the fungi, which consist only of fungous tissue.

Since the structure developed by this species is quite different from the stromata of the fungi, and particularly from that typical of the stromatic Sphaeriales, it is necessary to consider a question of terminology. How should the stroma-like pustule produced by *Melanotheca aggregata* be designated? The designation *stroma* cannot be applied, but the term *pseudostroma* (previously used by Wainio (1890) for the covering of the aggregate fructifications of certain genera, as *Graphis*, *Pertusaria*, *Trypethelium*, etc., which are similar externally but which have different microscopic morphology) might be used in this connection. The term *pseudostroma* would then come to have a specific meaning for the first time and would be defined as an aggregate of perithecia in a pustule simulating the true stroma of the fungi, the pustule being composed primarily of bark cells altered by fungal hyphae.

When *Melanotheca aggregata* has developed to the stage described one finds extensive pseudostromata composed of numerous perithecia (pl. 2, fig. 6). Each perithecium is a flask-shaped structure with a carbonaceous wall (composed of vegetative hyphae in connection with bark cells) and a loosely arranged mass of very slender ascogenous hyphae at the base. Numerous branches are sent out from this basal region (the paraphyses). They are themselves unbranched and they completely fill the perithecial cavity before any differing elements are noted. The hyphae are too small to distinguish whether or not septa might be present, but it is evident that they are multinucleate throughout the course of their existence.

After the paraphyses have filled the perithecial cavity the first ascus primordium can be noted. It may be distributed at random among the paraphyses and it usually originates near the center of the cavity. One cell near the tip of a hypha simply becomes much larger and is seen with a definitive nucleus.

The hypha from which this has arisen is similar to those which gave rise to the paraphyses—very slender, with no visible septa, and with several nuclei. Actual union of the nuclei has not been observed at this point but conditions approaching crozier formation are apparent, and all evidence points to the fact that a nuclear fusion must take place here. The young ascus enlarges rapidly, its nucleus increases relatively in size, and the cytoplasm becomes quite vacuolate.

As the number of asci increase a more or less definite hymenium is formed, and the hyphae at the base of the perithecial cavity become more compact. The hyphae are so small and the concentration of protoplasm is so great that the heavy stain that is taken obscures many details. As contrasted with the nuclei of the ascogenous hyphae, however, the definitive nucleus of the ascus is plainly visible.

Compared to asci in other members of the Trypetheliaceae those of *Melanotheca aggregata* are rather small, and the details of nuclear division are not exceptionally clear. In spite of this it is certain that the fusion nucleus undergoes three successive divisions resulting in the formation of eight free nuclei. Astral rays have not been seen but cleavage planes are fairly evident. Eight uninucleate spores are delimited from the epiplasm of the ascus and the process is evidently similar to that described by many workers for other Ascomycetes. By two subsequent mitoses, accompanied by cell-wall formation, a 3-septate spore, $12-18 \times 5-7 \mu$, is produced. The spore is brown at maturity.

Melanotheca cruenta (Mont.) Müll. Arg.—

This species has a thin thallus, a cortex $16-55 \mu$, a gonidial layer $10-45 \mu$, and a medulla varying in thickness. In most cases the medulla extends a considerable distance among the cells of the bark in which the plant grows—often to the extent of 12–16 cell layers. In some of the layers, and particularly in the uppermost, alteration of the bark cells from their normal condition is easily observed.

Ascogonia may be produced either above or below the gonidial layer. They are first seen as hyphal coils and they de-

velop in the same manner as those of *Melanotheca aggregata* described above. The carbonaceous wall of the perithecium becomes embedded in pseudostromatic tissue; it is composed primarily of vegetative hyphae but encloses a large number of altered bark cells. Such cells are not confined to the perithecial wall but extend in all directions, forming pseudostromata. Ascogenous hyphae arise in the lower portions of each perithecium and give rise to asci and paraphyses. The young ascus is uninucleate. Three successive nuclear divisions follow and eight spores are delimited. After the formation of the ascospore membrane the nucleus of each spore divides to form a 3-septate spore 20-35 μ in length.

The pseudostroma of this species may appear in varying shades of red, forming a striking contrast with that of *Melanotheca aggregata* which is quite black. The perithecia sometimes stand well exposed on the surface of the bark. At other times they are borne entirely submerged with only an ostiole projecting which is so minute that it can scarcely be seen. Young pseudostromata are sometimes covered with cortex and a gonidial layer but these structures have usually been shed in older material. Sometimes the pseudostromata are continuous and confluent; on a different type of bark, however, pustules readily form. The elevation of the pseudostroma seems to depend upon the nature of its substrate. Although the pseudostromata of *M. aggregata* show great polarity of aggregation, those of *M. cruenta* exhibit great variations, both in this regard and in other characteristics, resembling the variability of other groups of stromoid plants.

Melanotheca arthonioides (Eschw.) Müll. Arg.—

The cortex of this species is 5-45 μ thick and contains few distinguishable fungal hyphae. The gonidial layer is borne in the bark and varies from 5-35 μ in thickness. The medulla extends several cell layers in depth. The substrate is considerably modified by the activity of the fungal component of the lichen. Counts on the number and disposition of the cells of the bark disclose the probability that a number have been removed during the formation of the perithecial cavity. The

carbonaceous wall of the peritheciun is denser than in any species previously discussed, but in favorable sections it can be ascertained that the structure is composed largely of bark cells (pl. 4, fig. 6).

The perithecial initials and young perithecia undergo individual development, but the gradual expansion of the blackened zone of the bark cells unites adjacent ones into typical pseudostromata. Single perithecia can sometimes be found but they do not often occur. The cortex and gonidial layer rarely seem in intimate connection with any carbonized bark cells. Usually the contour of the bark is not appreciably modified by the pseudostromata, and in the specimens examined the perithecia were completely immersed in the substrate. The ascogenous hyphae, paraphyses, and the nuclear history of the ascus are similar to those of other species of the genus.

Melanotheca concatervans (Nyl.) Zahlbr.—

Macroscopically the thallus of this species appears rather thin, almost as though algae were lacking. Microscopic examination reveals, however, that the cortex is 15–25 μ in thickness; the gonidial layer 15–30 μ ; the medulla extending some distance farther. The perithecial initial is located deep within the bark (often below the gonidial layer); in its earliest stages it consists of a few coils of deeply staining hyphae in a spherical mass. Trichogynes have been observed; they are delimited slightly before the ascogenous hyphae appear. The early stages of the perithecial cavity are developed through the influence of the vegetative hyphae surrounding the perithecial initial, but the paraphyses sent out from the young ascogenous hyphae are responsible for its subsequent enlargement. At maturity the perithecia are embedded rather deeply in the bark, and the fungal hyphae exert visible effects on most of the upper cell layers. As each peritheciun develops, the zone of carbonized bark cells spreads toward all sides and results in typical pseudostromata. The details of development are similar to those of the three other species of *Melanotheca* discussed above.

TRYPETHELIUM

Trypethelium tropicum (Ach.) Müll. Arg.—

Interesting characteristics of the gonidial layer are shown by the material of this species. The algae develop very deep in the bark of the tree upon which the lichen is growing and may be present whether any fungal hyphae can be distinguished or not. As the fungus penetrates into the periderm the outer bark layers are sloughed off until the cortex consists of only one or two layers of bark cells surrounded by fungal hyphae and the gonidial layer lies very near the surface. The cortex is then 5–20 μ , the gonidial layer 10–30 μ in thickness. The ascogonia have been found when the thallus is in this condition. The perithecial initials are either intermingled with algal cells or are located just above the gonidial layer surrounded by cortical tissue. Trichogynes are delimited and the entire primordium is similar to the same structure in species of *Melanotheca*.

After the young perithecium is formed, however, further development differs materially from any species of *Melanotheca*. Additional fungal hyphae are built up on the exterior of the ascogonial coils and a relatively large hyphal mass is produced. The mass is brownish in young stages but soon becomes carbonaceous and increases in size during the growth and maturation of the ascogenous hyphae and asci. The structure formed is homologous with the perithecial walls of species of *Melanotheca* as the latter structures are interpreted in this paper. The perithecial walls are thus formed separately and above that portion of the bark in which the cortex and gonidial layer are located (pl. 3, fig. 3). The nearness of some of the perithecia to others results in a great many of them becoming united, but the polarity inducing this is not nearly so great as in *Melanotheca*. It would seem that little polarity exists in this species, since almost as many perithecia occur alone as in groups.

All lichenologists have not assigned the species discussed to the genus *Trypethelium* although most modern authorities

have done so, justifying such disposal upon macroscopic observation, for the masses of "united" perithecia are somewhat comparable in external appearance to the pseudostroma of *Melanotheca* (pl. 1, figs. 2 and 6). Microscopic examination discloses the fact that *Trypethelium tropicum* differs as fundamentally in its morphology from *Melanotheca aggregata* as the pseudostroma of *M. aggregata* differs from the "stroma" conceived in the minds of lichenologists as characteristic of the Trypetheliaceae. The "stroma" of *Trypethelium tropicum* is not composed of coalesced vegetative tissue unconnected with the perithecia, nor of altered bark cells, but of coalesced perithecial walls, homologous to the perithecial wall embedded in the pseudostroma of species of *Melanotheca*.

Trypethelium annulare (Fée) Mont.—

The perithecial initials of *T. annulare* are located farther below the surface of the bark than in any species of the genus examined. The gonidial layer, 10–35 μ in thickness, is often located eight to ten cell layers down and the ascogonia are borne below this layer. After the trichogynes disappear the ascogonia enlarge into ascogenous hyphae. Many of the bark cells around the young perithecium are rearranged and somewhat altered by fungal hyphae, though they never become dark and carbonaceous, and the expenditure of considerable force is a factor in the enlargement of the perithecial cavity. The perithecium is usually solitary, and its development is unconnected with that of any other. A carbonaceous perithecial wall may be conspicuous although it is often incomplete. The perithecium is embedded in cells of the bark. Such cells are almost normal in appearance and the structure formed, though similar in construction to species of *Melanotheca*, differs greatly in appearance (pl. 3, fig. 2). The extent of aggregation also differs from that genus for here many perithecia are solitary. It is interesting to note, however, that when two or more perithecia do occur in close proximity the cortical and gonidial layers are then considerably raised and hyphal threads extend among several loosened bark cells from one perithecium to the other. This does not often occur, and where possible the

cortex sags to its natural level before rising above the neighboring perithecium.

Although this species has usually been considered a member of *Trypethelium* there is really less reason for its placement there on the basis of our present system of classification than for *T. tropicum*, described above. The organism is somewhat similar to *T. tropicum* in its earlier stages of development. However, a great difference exists in that the perithecial initial of *T. tropicum* is found near the surface of the bark and the perithecial wall stands free at maturity, whereas in *T. annulare* the initials are located very deep in the bark with the result that the perithecia are also deeply buried. The fact that the perithecia are produced below the surface of the substrate is probably the factor that has allowed the classification of this species in the genus, for lichenologists looking at a specimen, even under magnification, might think the perithecia embedded in a common stroma rather than in the bark (pl. 1, fig. 1). The bark cells are arranged around the perithecia in a manner similar to the pseudostroma of *Melanotrichia*, but there is no carbonized alteration of these cells and the cortex and gonidial layers extend conspicuously throughout the structure. The "stroma" of this species is thus to be interpreted as vegetative lichen thallus and the perithecia are to be considered as merely immersed in the bark. The close proximity of occasional perithecia, however, shows a tendency that perhaps reaches a higher development in the species next to be discussed.

Trypethelium pallescens Fée—

As in *T. annulare*, the perithecial initials are formed unusually deep among the cell layers of the bark. They are formed below the gonidial layer, which is 11-25 μ thick, and covered by a cortical layer 15-45 μ in thickness. Perithecia are developed singly but considerably greater polarity of aggregation is evident than in any species of the genus discussed to this time. As the ascogonia develop and the perithecia expand, they raise, but do not rupture, the upper layers of the bark, and the bark cells below the fourth or fifth layers become

loosely arranged. The perithecia develop a carbonaceous wall formed entirely of fungal hyphae. The top layers of bark cells are separated completely along the area of polarity, and the cells just below these layers are forced apart so that they stand loosely arranged in a network of fungal hyphae (pl. 3, fig. 1). The entire body of the perithecium is located below the surface of the bark, which usually contains both cortical and gonidial tissues, but which remains unbroken itself.

The "stroma" of this species then consists of a raised pustule with cortical and gonidial layers on the upper surface, followed by a perithecial layer interspersed with a loose network of fungal hyphae between somewhat altered bark cells. This structure is quite different from anything previously described in this paper, and the author suggests that the term "substroma" be used to refer to it. The term will be defined as an aggregate of perithecia in a pustule, the pustule being composed as much or more of fungal tissue than of bark cells, with whatever bark cells are present being loosely and somewhat irregularly arranged. This structure is interpreted as derived from species similar to *T. annulare* where at times transition filaments were noted between perithecia which occasionally occurred in close proximity.

Trypethelium eluteriae Spreng.—

In this species the cortex is 24–60 μ , the gonidial layer 35–70 μ in thickness. The perithecial initials are formed below the gonidial layer and the polarity of their aggregation is even more pronounced than in *T. pallescens*; consequently the initials are clustered in groups. As the clusters develop the mass formed is so great that many of the bark cells above the primordia are sloughed off. Others become embedded in excess fungal hyphae in a manner similar to the bark cells in the substroma of *T. pallescens*. In this case, however, the perithecia are so close together and so near the surface of the bark that few bark cells can be enclosed (pl. 4, fig. 9).

Here, for the first time, we find a sort of "stromatic" structure which must be somewhat similar to that on which the lichenologist's concept of the Trypetheliaceae has been based.

At maturity a pustule composed primarily of interwoven hyphae is developed, within which perithecia are enclosed (pl. 1, fig. 4). The pustule stands fairly free on the surface of the bark and few bark cells are embedded in it (pl. 3, fig. 4). The author considers this an advanced substroma in contrast to the primitive substroma described for *T. pallescens*. His reasons for not calling it a true stromatic form will be given in the discussion. It is fairly easy to imagine a series of steps in the evolution of such a substroma, starting with the condition found in *T. annulare*, passing through *T. pallescens*, and ending in *T. eluteriae*. In this series the development of perithecia has been gradually transferred from below the bark cells to within a fungal matrix, the transition being due primarily to a gradual increase in the polarity of aggregation of perithecial initials.

TOMASELLIA

Tomasellia aciculifera (Nyl.) Müll. Arg.—

Cortical and gonidial layers of this species are very poorly developed. Filaments of *Trentepohlia* do not form definite algal layers but occur sparsely in isolated clumps. The perithecial initials arise three or four cell layers below the surface of the bark. Each perithecium begins development separately, but many of them become joined at a later stage and typical pseudostromata are then formed. Only five to ten perithecia are embedded in each pustule, but otherwise this species is similar to *Melanotheca* in "stromatic" morphology. The wall of the perithecium is incomplete and the ascogenous hyphae appear to arise directly upon bark cells. If the species of *Pyrenula*, represented in pl. 4, fig. 5, were pseudostromatic, a structure somewhat similar to that of this species would be observed.

LAURERA

Laurera madreporeiformis (Eschw.) Riddle—

The gonidia of this species are borne in groups a great distance below the surface of the bark. Often a layer 5–45 μ in thickness is formed, but the algae usually reproduce vigorously in clusters and relatively large assimilative areas are pro-

duced which push through the surface of the bark. In this process the top layers of bark cells are broken and the remnants sloughed off, leaving only fungal hyphae which form an amorphous crust representing cortical tissue.

Perithecial initials of this species are embedded in the bark above the gonidial layer and consist of several ascogonial coils. Trichogynes have not been seen. The initials are borne in fairly well-defined groups and typical substromata, similar to those of *Trypethelium eluteriae*, are finally formed (pl. 1, fig. 3). Bark cells fill the lower half of the substroma and a few are also embedded in the perithecial walls (pl. 4, fig. 1).

Laurera sanguinaria Malme—

The development of this species is similar to that of *L. madreporeiformis* except that the perithecial initials are usually borne below the gonidial layer. The latter is only 10–25 μ thick, and is not quite so extensive as in the preceding species. The substromata, however, are more widespread and are composed predominantly of fungal tissue (especially in the lower half of the structure). Conspicuous bark cells, arranged in their natural layers, however, are found above the perithecial walls (pl. 4, fig. 3). A typical substroma, similar to those of *Trypethelium eluteriae* and *Laurera madreporeiformis*, is formed.

BOTTARIA

Bottaria cruentata Müll. Arg.—

The cortex and gonidial layers of this species are relatively well developed, being 20–40 μ and 15–20 μ thick, respectively. The material referred to this species is interesting because it shows the most striking case of alteration of bark tissue that I have yet seen. The perithecial initials are borne extremely deep in the bark and the entire altered portion of the pustule may extend as far as 45 cell layers below the surface. The structure developed is similar to the pseudostroma of *Melanotrichia* and although the earliest stages in its development have not been found it was probably formed in a similar manner.

Bottaria must be considered a relatively rare genus, since

Zahlbruckner ('22, '31) listed only seven species. Evidence indicates that the material studied here might be a member of the Astrotheliaceae rather than the genus to which it has been assigned. The specimens, though, are identical with the material described by Müller-Argau (1885) for that species, and they are considered here as the only authentic material available for our concept of the genus. Other species have at times been incorporated in *Bottaria*, as *Anthracothecium ochraceo-flavum* and *A. pyrenuloides*. These species are illustrated in pl. 4, figs. 7 and 8, but at times aggregations of perithecia are found whose macroscopic appearance would simulate the condition found in *Trypethelium annulare*.

CYTOTOLOGY

Since cytological similarities are indicative of probable relationships it seems desirable that the cytological phenomena in the asci of these lichens be compared with those described for analogous fungi. No similar study has been made on any member of the Trypetheliaceae; the Moreau's ('32) observations upon *Dermatocarpon* constitute our only knowledge of such processes among the Pyrenocarpeae.

Division stages are rarely encountered in sections of members of the Trypetheliaceae made from material killed at random intervals. The author was fortunate, however, in securing material of *Trypethelium annulare* which was more favorable for study and which has yielded the observations recorded below. A critical analysis of chromosome numbers and morphology, with a discussion of the mechanism of spore delimitation, is reserved for what is hoped may be a more comprehensive treatment at a subsequent time. The author is primarily interested in showing how closely the processes approach those known for the fungi.

Asci and paraphyses arise from a layer of ascogenous hyphae located at the base of the perithecial cavity. The layer is so dense and the elements are so small that it is difficult to trace their course in serial sections. The outgrowths from the ascogenous hyphae all appear multinucleate, and in most cases

it is impossible to detect any differences in these nuclei. Occasionally, however, the tips of the shorter ascogenous hyphae appear somewhat recurved and the second nucleus is slightly larger than the others. It is such a short transition from this condition to the young ascus that the author is inclined to interpret the penultimate nucleus as a fusion nucleus and the recurved hypha as a crozier. Many transitions occur, not so easy to interpret, but a uninucleate ascus always results whose nucleus, contrasted to those of the ascogenous hyphae, is very distinct. The resulting definitive nucleus does not at first differ in constituency from any of the nuclei originally present, but it is slightly larger. The nucleus undergoes an increase in size before it divides and the ascus shows a corresponding change. While the nucleus enlarges it becomes less dense and a chromatic reticulum and dark-staining nucleolus show clearly. Usually chromatin threads are attached to the nucleolus. Spireme threads are organized. The nuclear membrane disappears shortly after this stage and subsequent development remains intranuclear throughout the division. After the disappearance of the membrane small chromatic fibers attached to the nucleolus radiate into the nuclear area. The nucleolus disappears and the spindle develops in the same area in late prophase. The spindle is located in the center of the ascus and is much longer than in either the second or third division. Chromatin globules are apparent at intervals on the spindle fibers. Astral rays are rarely seen.

Two nuclei reorganize completely from the first division. No cell wall is formed. The nuclei are much smaller than the definitive nucleus. The nucleolus, though smaller, is just as conspicuous. Numerous chromatic granules are present in the nuclear sap. Only a slight interval exists between the first and second divisions and the two nuclei divide simultaneously. The spindle is rather short; astral rays are not seen.

Four nuclei, similar in size and appearance to those resulting from the first division, reorganize from the second division. Some time seems to elapse between the second and third divisions, but the nuclei do not increase in size; they simulate

resting nuclei. A conspicuous chromatic reticulum is present in the nuclear sap. The four nuclei divide simultaneously.

The spores are delimited immediately after the third division. Astral rays have not been correlated with this process. Definite cleavage planes seem evident as soon as the ascospore initials become distinct, and the final delimitation from the epiplasm of the ascus is due to their rapid development.

By virtue of the parallel arrangement of the spindles of the third division the young ascospores occupy an oblique position in the ascus. Growth of the ascus and ascospore is at first very rapid but slows down considerably as the more mature stages are reached. The uninucleate spore initial undergoes mitosis, accompanied by the septation of the spore. The spore and the ascus increase considerably during this division and the bicellular spore is quite vacuolate. The membrane that surrounds the spore has increased in thickness and is now a well-defined spore-wall. A second mitotic division occurs after which septa are again formed. During the last division both the ascus and the spores have increased greatly in size; the latter have secreted thicker walls. Eight three-septate spores are always produced in each ascus.

LICHEN ACIDS

A view frequently expressed is that the lichen acid is a product peculiar to the lichen thallus and one that has been built up by the continual association of fungus and alga over a long period of time. Smith stated ('21) that their occurrence is of particular significance because of the fact that they have been found only in lichens and that they have been found in the majority of lichens examined.

Tests for the presence of these substances are based upon color reactions induced by certain chemicals. Such practice was first suggested by Nylander (1866, 1867) who recommended calcium hypochlorite and potassium hydroxide for that purpose. Both of these have been universally used since that time. In addition Asahina ('34) has recently proposed

the use of paraphenylenediamine, and this reagent is now being widely used.

To provide data which might have some validity in indicating the relative abundance of lichen acids among the families considered in this paper the reaction of several pyrenocarpous lichens with certain chemical reagents is given in table I. Attention will be called to this data in the discussion below.

TABLE I
REACTIONS OF THE THALLI OF SOME PYRENOCARPOUS LICHENS
WITH CHEMICAL REAGENTS

Species	Calcium hypochlorite*	Potassium hydroxide	p-phenylenediamine
<i>Pyrenula nitida</i>	-†	-	-
<i>Pyrenula laevigata</i>	-	+	-
<i>Pyrenula Coryli</i>	-	-	-
<i>Porina chlorotica</i>	-	+	-
<i>Porina mastoidea</i>	-	+	-
<i>Pseudopyrenula Papula</i>	-	-	-
<i>Clathroporina amygdalina</i>	-	+	-
<i>Arthopyrenia punctiformis</i>	-	-	-
<i>Arthopyrenia rhyponta</i>	-	-	-
<i>Anthracothecium ochraceoflavum</i>	-	+	+
<i>Anthracothecium pyrenuloides</i>	+	+	-
<i>Melanotheca aggregata</i>	-	+	-
<i>Melanotheca cruenta</i>	-	+	+
<i>Melanotheca arthonioides</i>	-	-	-
<i>Melanotheca concatenans</i>	-	-	-
<i>Trypethelium eluteriae</i>	-	+	-
<i>Trypethelium ochroleucum</i>	-	+	-
<i>Trypethelium tropicum</i>	-	-	-
<i>Trypethelium pallens</i>	-	+	-
<i>Trypethelium virens</i>	-	+	-
<i>Trypethelium annulare</i>	+	+	-
<i>Tomasellia aciculifera</i>	-	+	-
<i>Bottaria cruentata</i>	-	+	+
<i>Laurera madreporialiformis</i>	-	+	-
<i>Laurera ambigua</i>	-	-	-
<i>Laurera sanguinaria</i>	-	+	+

* Calcium hypochlorite = saturated aqueous solution; potassium hydroxide = 7% aqueous solution; p-phenylenediamine = 0.1 g. in 5 cc. 95% alcohol.

† + = visible color change; - = no reaction.

SPORE GERMINATION

The difficulty of growing lichens in artificial culture is one of the reasons often advanced to support the belief that they are so distinct physiologically as to be monophyletic in origin. As far as the author has been able to ascertain no attempts have been made to culture members of the Trypeteliaceae.

Spore-germination tests on several members of the family were made in a wide range of nutrient solutions and on various agars, following the method reported by Wehmeyer ('23). All cultures were kept in a well-lighted room at 20-25° C. Little difficulty was experienced in germinating spores within three months of the date of collection of the material although the percentage of germination was never high. Spores of material dried for more than three months failed to germinate.

Trypetelium and Melanotheca: Spores of *Trypetelium pallescens*, *T. ochroleucum*, *T. annulare*, *T. eluteriae*, *T. tropicum*, *Melanotheca aggregata*, and *M. cruenta* have been successfully germinated and (with the exception of *T. ochroleucum*) mycelium resulting has been grown in culture. In *Melanotheca aggregata* considerable growth on bark has taken place. These species possess phragmospores. The terminal cells are invariably the first to germinate, and this often takes place within forty-eight hours. Germination of the central cells is not uncommon, although this usually does not occur until at least twenty-four hours later. Young germ-tubes are non-septate; septation does not occur for at least one week.

Laurera: Spores of *Laurera madreporialiformis* and *L. megasperma* have been successfully germinated. Each merispore may give rise to a germ-tube. A rather large number of germ-tubes per spore may occur but three or four is the usual number seen. When fresh material is used germination may begin within forty-eight hours. The germ-tubes remain non-septate for one or two weeks, after which time septa are formed and lateral branches may develop.

Transference of germinating spores of either group to agar plates yields a rather slow-growing mycelium. Muriform

spores rarely progressed beyond the germ-tube stage. Neither asexual spores nor perithecia have been produced in cultural studies. Furthermore, the mycelium, whether allowed to remain on the original medium or transferred to new substrata, failed to live more than six months.

The cultural work undertaken on members of the Trypetheliaceae can be summarized as follows: (1) ascospores have been successfully germinated in three genera and ten species; (2) the spores, if taken from fresh material, show a low percentage of germination but produce mycelium under a varying number of conditions; (3) phragmospores usually germinate from the terminal cells only, but germination of the central cells is not uncommon; (4) each merisporule of a muriform spore is a potential germ-cell; (5) mycelial growth on agar cultures is exceedingly slow.

SUBSTRATE RELATIONS

Lichenologists who have paid particular attention to the attachment of bark-inhabiting members of the higher lichens (foliose and fruticose forms) have agreed that if the rhizoids penetrate below the surface of the bark they do not extend far into the periderm (Schwendener, 1860, 1863, 1868; Lotsy, 1890). Bornet (1873) described the penetration of the fungus and alga of crustose forms into the periderm but did not mention their action on the substrate. According to Frank (1877), lichen hyphae and species of *Trentepohlia* dissolve the cellulose of the periderm cells and utilize nutritive material obtained from this action. Lindau (1895) vigorously opposed Frank's conclusions, stating that the organisms could neither penetrate the periderm cells nor dissolve the cellulose available. Fink ('13) gave a general discussion of the relation of lichens to their substrata and made the following remarks in that connection (p. 148):

It is certain that hypophloedal lichens which live in the periderm for a year or more outside the relation with an algal host must take nourishment from the periderm, though they do not dissolve sufficient material from the periderm walls to be detected by microscopic examination. So we must believe

that these plants secure nourishment from the periderm without entering the cells or producing appreciable diminution in walls or other effects that can be detected without chemical analysis.

Bioret ('22) examined the thalline structure of bark-inhabiting Graphidaceae without reporting alteration of the bark cells by members of the group.

It is very difficult to say what the relation of the Trypetheliaceae to their substrata might be. Each species should be considered as a specific case. Proof that food material is actually obtained from the bark would be best if based upon chemical analyses of the bark cells before and after growth of the lichen, but this is almost beyond technical possibilities. Overwhelming evidence points to the fact that the lichens are not parasitic on the trees, although the author has often heard Dr. C. W. Dodge point out that pyrenocarpous lichens on trees that had just been cut would soon discharge their spores. I am able to confirm these observations and to state further that I have collected good fruiting material of this family only upon living trees. Perhaps the moisture ordinarily present in the bark is a necessary factor for vegetative growth.

Whether or not some of the plants acquire a portion of their food saprophytically, however, is another question. Admittedly one hesitates to make such an assertion—for a statement would be difficult to prove from purely anatomical considerations. Attention might be called to the fact that the bark cells composing the pseudostroma of species of *Melanotheca* are altered by the fungus. The alteration does not seem to be purely physical, but a definite carbonization, a chemical alteration, also occurs. This same condition has been observed in *Tomasellia* and *Bottaria*. In other genera evidence is not so striking. Although the bark cells in the substromata of *Trypetellum pallescens*, for example, have been separated and certainly look as though something had happened to them, they are no darker or more altered than those of adjacent bark.

If the plants should prove selective in substrate among trees having the same characteristic bark anatomy the fact might suggest preference for a certain type of food. Plants collected

in Mississippi and Louisiana have been studied in this regard. Only those species collected ten or more times, backed by herbarium specimens of both lichen and substrate, are reported here. Of the ten species of the Pyrenulaceae and Trypetheliaceae which fulfill these requirements, eight have been collected on a single genus. Two other species have been collected on three genera but variations in the anatomical characteristics of the pseudostromata, cortex, and gonidial layer suggest that two or even three species might be involved in each case. More data covering a larger area must be accumulated, but it is interesting to note that preliminary study in a relatively limited locality indicates considerable lichen-substrate specificity.

The author is inclined to agree with Fink's ('13) generalization for certain hypophloedal lichens, as far as the Pyrenulaceae and Trypetheliaceae are concerned, i.e., that some of these organisms must acquire a portion of their nourishment from their substrata.

NOTES ON THE PYRENULACEAE

The development of members of the Trypetheliaceae is very similar to that reported by Baur ('01) for *Pyrenula nitida*. Since this similarity is so great as to postulate close relationship the morphology of species classified in the Pyrenulaceae has been studied. In this section the author's notes on the development of *Pyrenula nitida* will be compared with Baur's description. The microscopic morphology of some other species of the family will be compared so that some concept of the degree of development of certain characters (particularly the gonidial layer and the extent of aggregation of the perithecia) may be obtained.

Pyrenula nitida (Schrad.) Ach.—

According to Baur ('01), the perithecial initials are first seen as hyphal knots located at about the same height as or slightly below the gonidial layer. In the material studied by the author they were found three and four cell layers below

any algae present. Baur observed that early in development, even before the differentiation of the ascogonia, polarity becomes evident and the hyphal knot grows toward the exterior, the ends of the hyphae boring through the bark and reaching the surface. He compared these hyphae with the first paraphyses of *Pertusaria*, *Physcia*, etc., and suggested that it was their function to clear the way toward the exterior. In material studied by Baur the peritheciun increased in size and resulted in a stage in which the form and almost the size of the mature fructification were reached before ascogonia were delimited. My material confirms these statements except that the ascogonia were produced in the early stages of perithecial expansion. After ascogonia, trichogynes are formed which grow toward the exterior and project beyond the surface of the bark. As was emphasized for members of the Trypetheliaceae, the perithecial cavity originates through the action of vegetative hyphae and trichogynes emerge through an ostiole before any ascogenous hyphae arise. The perithecial wall is not often composed of disintegrated substrate but the base of this wall is coalesced with dark, carbonaceous bark cells. A peritheciun is covered by or partly immersed in the substrate, depending upon its state of maturity. In youth the uppermost bark cells cover it; later it breaks halfway through. The perithecia are almost spherical, 300–900 μ in diameter, and sometimes are clustered, showing a tendency to aggregate in groups. The perithecial wall is complete. The development of this organism is so strikingly similar to members of the Trypetheliaceae as to be almost identical.

Other Species:—

In *Pyrenula Coryli* Mass. the gonidia are exceptionally sparse; I have found them very infrequently and only in the neighborhood of perithecia. The gonidial layer of *Pyrenula laevigata* Arn. is very variable; often, however, it consists of only a single cell embedded in a mass of hyphae. The thallus of *Arthopyrenia punctiformis* Mass. is composed primarily of a black layer or a black scale over the surface of the bark; gonidia

are rarely found and in all cases observed consist of single cells. In the three species listed in this paragraph the perithecia never show any transitions toward a pseudostromatic or substromatic structure.

In *Anthracothecium ochraceoflavum* (Nyl.) Müll. Arg. and *A. pyrenuloides* (Mont.) Müll. Arg., on the other hand, well-developed gonidial layers are found. In *A. ochraceoflavum* the cortex is 15–65 μ and the algal layer 5–20 μ thick. *A. pyrenuloides* has a cortex 20–55 and a gonidial layer 10–20 μ thick. In both species the perithecial initials are borne below the surface of the bark, and the perithecia may arise near each other or be widely separated. These transitions make the generic determination of the species a matter of opinion, for it would seem from macroscopic appearance that the specimens examined could equally well be assigned to *Bottaria*.

Anatomical observations on the species mentioned, as well as on others whose descriptions are omitted, support the following suggestions: (1) some members of the Pyrenulaceae are very primitive lichens as far as the relation of the fungus to the alga is concerned; (2) there are tendencies to evolve aggregated perithecia and a well-developed gonidial layer in the family; (3) some species show a morphology similar to that of species assigned to the Trypetheliaceae.

DISCUSSION

The morphology displayed by members of the Trypetheliaceae makes necessary the discussion of a descriptive term that has been used in connection with the group. This object of particular concern is the term *stroma* of which recent elucidations have been given by Orton ('24), Wehmeyer ('26), and Miller ('28a) for certain fungi. A *stroma* is ordinarily defined as a fungus body formed of coalesced hyphae that does not arise as the result of a sexual stimulus. Although admitting necessary broadness in defining this structure it hardly seems logical to accept a definition such as the above which would place all paraplectenchymous and pseudoparenchymous tissues in stromatic genera whether connected with fructifications or not.

Examples are: the cortices of many lichens, the rhizomorphs of Basidiomycetes, sclerotia, etc. Miller's paper ('28a), in which he implies that all Sphaeriales are partially stromatic, is based upon important theoretical considerations, but actually the best that he does to limit the term is to consider coalesced hyphae belonging to the haploid generation stromatic tissue.

The designation *stroma* has been applied to structures in many families and many genera, often without sufficient knowledge of the microscopic morphology of the structure involved and without a basis from developmental morphology. The term was first used in connection with the structures on or in which the perithecia of *Sphaeria* are borne (Persoon, 1796). Five years later Persoon (1801) employed the term only in connection with a certain group of his genus *Sphaeria*, the examples given now being assigned to *Cordyceps*, *Xylaria* and *Hypoxyton*.

Xylaria, *Hypoxyton*, and some of their relatives have been shown to have a similar type of development in which the tissue bearing perithecia is divided into two layers (Füisting, 1867; Lupo, '22; Miller, '28a, '28b; Brown, '13; Dawson, '00; Wehmeyer, '26). Conidia are usually produced from an outer layer; subsequently perithecial initials develop near the outer portion of the inner layer. Such correlated characters have given rise to the opinion that these genera must be members of natural groups, and these groups have been consistently called "the stromatic Sphaeriales" and "the stromatic Hypocreales." There would be some advantage on the basis of exact usage to limit the term *stroma* to those groups which possess the following combination of characters: (1) perithecia borne in a mass of interwoven vegetative tissue; (2) mass divided into two layers; (3) asexual spores produced by the outer layer; (4) perithecial initials developed from the outer portion of the inner layer. The structure could then be definitely delimited on the basis of a combination of fairly easily observed microscopic characters.

Although some of its relatives do, *Cordyceps* does not possess the correlated characters mentioned above (Varitchak,

'31; Jenkins, '34). In *Cordyceps* the perithecia are borne in a mass of purely vegetative hyphae, and current usage perhaps demands that this structure also receive the appellation *stroma*. The separation of "stromatic" forms from their nearest intergrading relatives is a difficult problem. The term *stroma* has been applied to so many structures that only one with a conservative attitude and proper acquaintance with all forms involved should try to limit it, but one set of the near intergrades must be discussed because it occurs in the group studied here. The author feels that the term *stroma* was never meant to apply to structures which were not purely fungal in nature, as is the case in members of the Trypetheliaceae. Even though one might claim the presence of bark cells relative and contend that pustules *almost* devoid of bark cells are entitled to be called stromata, the question of their separation from structures with more bark cells (*Trypethelium pallescens*, for example) becomes a matter of great difficulty. Here there would be great advantage, particularly as far as any phylogenetic significance attached to the term is concerned, to have the structure based upon a combination of characters as was suggested above, rather than upon a single feature. If the meaning of the term is to be at all relative, however, current usage would seem to demand at least that a stroma be composed entirely of fungal tissue, rather than to admit that structures containing bark cells could come within the scope of the term. The latter alternative would leave open the possibility that such forms as *Melanotheca aggregata* (where the "stroma" is composed primarily of altered bark cells) could be called stromatic. The developments of the pseudostroma of *Melanotheca* and of the stroma of *Hypoxyylon* are so different that the application of the same term to the structures in which their perithecia are borne seems absurd.

For the reasons given I contend that a true stroma has not yet been found in the Trypetheliaceae. Following such reasoning I have felt it necessary to define two other terms on the basis of microscopic morphology for the more accurate description of members of that family—and perhaps of other organ-

isms that will be found to simulate the formation of a stroma on macroscopic appearances. These are: *pseudostroma*—an aggregate of perithecia in a pustule, the pustule being composed primarily of bark cells altered by the fungus; and *substroma*—an aggregate of perithecia in a pustule, the pustule being composed of as much or more of vegetative hyphae than of bark cells. That there are transitions between non-stromatic, pseudostromatic, substromatic, and possibly stromatic forms is of course inevitable, but the recognition of the tendencies of evolution within various groups makes their distinction important.

The occurrence of various types of "non-stromata" and of intermediate transitions between these and substromata within generic groups (as the four types of development described in *Trypethelium*) indicates that we must regard the taxonomy of the Pyrenulaceae and Trypeteliaceae as in an unsettled state. Opinions on the limitations of the genera involved are withheld pending a taxonomic revision of the group.

Almost all investigators throughout the history of lichenology have recognized the aggregation of perithecia into a "stroma" as a matter for family distinction (see p. 2). This has resulted in placing *Melanotheca*, *Trypethelium*, *Tomasellia*, *Laurera*, and *Bottaria* in a single family, the Trypeteliaceae. Exceptions to this practice have been proposed by Wainio (1890), who considered the above genera as subgenera of the corresponding genera of the Pyrenulaceae, and by Watson ('29), who distributed the same genera among two different families, the Arthopyreniaceae and the Pyrenulaceae, depending upon the shape of the spore partitions and the nature of the paraphyses. Zahlbruckner ('26) and Keissler ('37) considered the Trypeteliaceae a natural family. Their reasons for such treatment give a forceful conception of the status of the knowledge of the morphology of its members previous to the publication of this paper. They merely imply that since the character of the "stroma" plays such an important part in the division of lower groups in the Pyrenomycetes it should

likewise be permissible to do the same thing among lichens—at least as long as nothing certain is known about the development of the lichen “stroma.”

In this paper the morphology of this so-called stroma has been described for several species at present classified in the Trypetheliaceae and some of the uncertainty with regard to its origin and development has been removed. Of the twelve species which have been most carefully studied only three have been shown to possess the morphology considered characteristic of the Trypetheliaceae. Four species of *Melanotheca*, and one each of *Tomasellia* and *Bottaria* are pseudostromatic. Three species of *Trypethelium* have not evolved well-developed substomata. Only *Trypethelium eluteriae*, *Laurera madreporiiformis*, and *Laurera sanguinaria* possess the latter structures. Future investigation will add more species to each group, but the recognition of these divergent types of “stromatic” morphology and of the transitions between them is one of the chief contributions of this paper. In several species perithecia are borne in a definite plectenchymous tissue but all intermediate types and transitions from merely immersed to pseudo- or substromoid and from solitary to aggregated perithecia have been found, not only within the family, but also within some of the recognized genera. Other points are also pertinent here: (1) The spore characters are extremely divergent. The present treatment of these genera postulates the aggregation of perithecia into a pustule as of more phylogenetic value than the difference between a dark, elongate spore with lentiform partitions (*Melanotheca*) and a hyaline, muriform spore with cuboid partitions (*Laurera*). Developmental studies upon the organisms involved have disclosed the variation in pseudo- and substomata and have shown that such is not the case. (2) The absence of one-celled spores and the prevalence of dark spores indicate that the Trypetheliaceae as at present conceived includes genera that are very advanced from the standpoint of the fungal component. Altogether this evidence is sufficient to show that the Trypetheliaceae as delimited by Zahlbruckner, Smith, Keissler, and others does not bring together closely re-

lated forms and that further search should be made to find a proper place in which the various genera might be disposed in a more natural system.

In searching for a place to dispose of these genera one would naturally consider the fungi, particularly the sphaeriaceous forms. It has already been pointed out that they cannot be placed with the group where they have often been associated on theoretical grounds, the "stromatic Sphaeriales," because: (1) The large, septate spores of the lichen genera are aberrant in series with the small non- or one-septate spores of the fungal groups. (2) Correlated characters such as the production of conidia from a well-defined ectostroma and the origin of perithecial initials in the entostroma do not occur in the Trypeteliaceae. (3) Bark cells occur in the pustule containing perithecia. A true stroma, therefore, is not produced; pseudostromata and substromata only occur.

There is no doubt but that the structure of the perithecium of these lichens simulates the same structure in the Pyrenomycetes, and the asci of the two groups are almost identical. The asci enclose eight spores delimited from the protoplasm of the ascus after three successive divisions of a definitive nucleus. The ascus of the Pyrenocarpineae is so similar to the ascus in the Pyrenomycetineae that the common origin and consequently the monophyletic divergence of their members must be assumed. Granted that the members of the Trypeteliaceae (and most other lichens) should be considered members of the Ascomycetes rather than as a class coordinate in rank with them, the problem becomes that of deciding just how divisions should be drawn in that group.

An overwhelming mass of evidence indicates the close relationship of pseudo- and substromatic species with plants classified in the Pyrenulaceae. This could even be assumed from theoretical considerations, for according to Zahlbruckner's ('26) classification, the group, if treated as lichens, must be attached to this family simply because no pseudostromoid or substromoid lichens have been described with *Palmella* or *Protococcus* gonidia. Factual evidence is presented through

the similarity of the manner of development of the Trypetheliaceae with that of *Pyrenula nitida* (Baur, '01). This similarity is evident in the ascogonia, trichogynes, perithecia, etc., and suggests that the two families be united. Since numerous transitions can be found between the "stromatic" and "non-stromatic" lichens, particularly with reference to the degree of aggregation of the perithecia, this disposal would obliterate the present confusion caused by using this character as a basis for family distinction. Furthermore, the spore forms, though differing as greatly within the family as before, can now be tied up with a phylogenetic scheme, the progression taking place both with reference to the degree of pseudo- and substromatic development and to the increasing septation of the spore. The lines of evolution can also be kept distinct with reference to the shape of the spore cells and the color of the spores.

For the above reasons the author prefers to regard the pseudostromoid and substromoid genera of the pyrenocarpous lichens as advances from simpler lichens usually classified in the Pyrenulaceae and to consider the genera of the Trypetheliaceae more logically placed as terminal members of the Pyrenulaceae. Thus, *Trypethelium* is regarded as having been derived from *Pseudopyrenula*, *Melanotheca* from *Pyrenula*, *Tomassellia* from *Arthopyrenia*, etc. Such an arrangement postulates that evolution in the group has proceeded from forms with simple spores, undifferentiated thalli (in the sense that neither a definite cortex nor a well-defined gonidial layer is evident), and single perithecia to more advanced forms with septate-elongate or muriform spores, well-developed cortices and gonidial layers, and a tendency toward the aggregation of the perithecia.

One is greatly impressed by the fact that some of the species examined, e.g., particularly *Pyrenula Coryli* and possibly *Arthopyrenia punctiformis*, lie on the very border-line between the fungi and the lichens. In many places no algae can be found in their thalli. In other species where algae are not often found the gonidial layer may sometimes be relatively well developed. I have found several cases where perithecia

occurred 2 mm. to 2 cm. distant from the vegetative portion of a thallus. These transitions indicate a variability in the relationship of the fungus with the alga and suggest the possibility that in some cases the fungus might be able to live without the alga, utilizing the cells of the bark directly for nutritive purposes.

In all species the thallus arises from a germinating spore, and in the beginning it must act as a saprophytic fungus growing upon wood. This process has been followed experimentally with *Melanotheca aggregata*. The algal colonies are enclosed and the thallus is formed only at a later date. Thus it seems that the pyrenocarpous lichens mentioned must spend a portion of their life as purely saprophytic fungi; the other is spent in combination with an alga.

Lichenologists have made much of the mode of nutrition of the lichen and refer to its strict symbiosis as a claim for phylogenetic distinctness. In addition to the points noted above it seems fairly evident that in some species of the Trypetheliaceae the fungal component can utilize tissue of the substrate after combination with the alga. Attention has been called to the fact that the bark cells are altered in a great many species. Particularly striking examples may be found in the pseudostromata of species of *Melanotheca*, *Tomasellia*, and *Bottaria*, where chemical changes occur and the resulting structures consist primarily of carbonized bark cells.

These observations, with certain facts to be discussed below, have given rise to the opinion that the Pyrenulaceae is a relatively recent development in the phylogeny of lichens. Apparently those species on the border-line between the fungi and the lichens do not require algae for their development, and hence they must be able to obtain some food saprophytically from their substrate; an undoubted fungal or primitive character as far as lichens are concerned. Whether some of the substromatic species obtain food from the bark is very difficult to ascertain, but some of them do still retain the ability to alter the bark cells. Although the utilization of food produced by the alga is somewhat more advanced than the state displayed by saprophytic fungi, the advance is hardly to be con-

sidered as great as in those species where the bark is unaltered by the fungus.

Soredia, which are distinctive marks of vegetative evolution in other groups of the lichens, have not been found in the Pyrenocarpeae. Their absence would postulate that the entire tribe had formed the symbiotic relationship with the algae in relatively recent time. Other significant facts pointing toward this same conclusion are: (1) there are few gelatinous (blue-green) forms in the same group; (2) very few foliose and fruticose genera have been described in the group; (3) the number of pseudostromatic and substromatic forms is small when the group is contrasted with the fungi.

Wehmeyer's ('26) ideas with regard to the evolution of a stroma can be followed in the Pyrenulaceae. This gives additional support to the conception advanced above:

The stroma has arisen in the Sphaeriales from simple Pyrenomyctes in which perithecia were immersed in the host or substratum tissue. . . . The first evidence of a primitive stroma appears as a blackening of the surface of the substratum. . . . The next step is the proliferation of the mycelium within the substratum. (See p. 580 for exact statements.)

Species similar to *Pyrenula Coryli* represent the stage in which the perithecia are immersed in the substrate; species similar to *Melanotheca aggregata*, the stage in which the surface of the substrate is blackened; species similar to *Trypethelium eluteriae*, the stage in which the mycelium has proliferated into a substroma. Differentiation into ecto- and entostroma, however, has not yet taken place and this group has, therefore, not evolved as highly as correlated groups of the fungi.

Certain conflicting evidence can also be explained on the assumption of recent symbiotic union in this group: i.e., the fact that the genera concerned present some rather advanced characters with regard to the fungal component (spore septation, size, and color) but some very primitive ones from the standpoint of their thalline characters (development of a cortex, presence of foliose and fruticose forms, absence of gelatinous forms, etc.). The origin of the symbiosis of Pyrenulaceae would be sought among rather advanced fungal genera.

Lichenologists have pointed out the characteristic disposal of the lichen acids as an aid in establishing the great antiquity of the lichen thallus. It seems that members of the Pyrenocarpineae are not nearly so rich in lichen acids as are some of the other lichen groups. In 1907, Zopf did not record a single lichen acid of known chemical composition from the Pyrenulaceae, and to the best of the author's knowledge none has been isolated since that time. Perhaps this scarcity of knowledge is correlated with their less frequent occurrence. The application of chemical reagents indicates that they do occur, but they seem more abundant in advanced groups (see table 1). Few of the "border-line" species gave reactions with either calcium hypochlorite, potassium hydroxide, or paraphenylenediamine—forms with well-developed gonidial layers being more abundant among those that did do so. If such crude tests as have been made are indicative of the presence of lichen acids (and they usually detect a great many of them) this fact seems of some significance. One cannot hold all lichen thalli to be ancient in origin simply because some species possess lichen acids, nor does it follow that all species without them are primitive. But if the presence of lichen acids be an advanced character in this group the data at hand support the suggestion that the "border-line" lichens are primitive and that other forms are more advanced. Although the author would agree with other lichenologists that the variety and specificity of the lichen acids, coupled with the many changes in the vegetative thallus of such groups as the Cladoniaceae, Parmeliaceae, Usneaceae, etc., certainly attest to the great antiquity of those families, the evidence found in the Pyrenulaceae favors the hypothesis of the recent association of the fungus with the alga.

One fact which does not favor such an assumption is the lack of known asexual spore forms in the Pyrenulaceae. Of course, these have not been determined for a great many Ascomycetes, but since the spores and resulting mycelium of advanced members of the family can be cultured it seems as though the primitive members of the family should have asexual spores. They

were not produced in six months of culture but varying conditions might modify the results obtained.

Miller ('28a) published an important paper from the standpoint of theoretical mycology in which he distinguished the Dothideales and the Sphaeriales as follows: Sphaeriales, characterized by a diploid perithecial wall, lack of pseudoparenchyma in the perithecial centrum, true paraphyses and periphyses, concave hymenial layer, and ostiole schizogenous; Dothideales, with no diploid perithecial wall, pseudoparenchyma in the perithecial centrum, no paraphyses and periphyses, concave to flat to convex hymenial layer, and ostiole lysigenous. The paper is also of interest because of the discussion of such terms as stroma, ostiole, perithecial wall, paraphyses, etc. Since the author is suggesting that for the present the Pyrenulaceae be considered members of the Sphaeriales, attention must be called to the fact that some of the characters listed cannot be easily ascertained for the Pyrenulaceae.

The specimens examined in this study usually gave rise to the ostiole before the formation of the ascogenous hyphae, and trichogynes projected through the opening so formed. It is more likely that this opening persists until maturity than that it is closed after the trichogynes disappear, making necessary the formation of another ostiole at maturity. Some evidence also exists that bark cells are digested by certain species during the formation of the ostiole. In this connection it is interesting to note that de Bary (1884, p. 207) stated that the ostiole is predominantly schizogenous in species of *Sordaria*, *Melanospora*, *Claviceps*, *Epichloë* and *Eutype*, but lysigenous in *Diatrype*, *Verrucaria*, *Endocarpon*, *Pyrenula*, and *Massaria* (Füisting, 1868). Dodge ('37) reported lysigenous ostiole formation in a species of *Leptosphaeria*.

The presence, absence, or nature of the paraphyses has been used taxonomically in the Pyrenulaceae to a considerable extent. In this family branched or unbranched paraphyses grow out from the ascogenous hyphae into the perithecial cavity. The small size of the component elements makes it difficult to ascertain whether the structures are diploid or multinucleate,

for septa cannot be distinguished. If a diploid membrane exists independently of the paraphyses surrounding the asci it is completely fused with bark cells, carbonized haploid hyphae, or is very difficult to see. Periphyses have been hard to demonstrate. Paraphyses are usually present in young, and absent in old material, so that their presence or absence is not essentially a good taxonomic character. It seems significant that after the maturation of the spores the paraphyses (like the membranes of the asci) usually disappear.

SUMMARY

(1). Previous to the publication of this paper no developmental study of any lichen assigned to the Trypeteliaceae had been made.

(2). Details of development are recorded for species assigned to the five older genera considered in that family. No material of *Trypeteliopsis*, a recently described monotypic genus from Japan (Asahina, '37), has been available for examination.

(3). The development of *Melanotrichia aggregata* is described from the germination to the maturation of the ascospore. In culture the spore gives rise to mycelium that may live some time without the presence of an alga. In nature, however, the fungal component contacts an alga early in its growth and a lichen thallus is formed. Ascogonia provided with trichogynes are produced and spermagonium-like structures have been found. No evidence for the fusion of spermatia with trichogynes could be seen. The perithecial primordium consists of several ascogonia surrounded by a sheath of vegetative hyphae. The gametophytic tissue is active in cutting out the perithecial cavity and in the formation of the ostiole. The ascogenous hyphae give rise to branches, some of which ultimately produce asci. The cytological phenomena involved in the production of ascospores are essentially the same as those described for other Ascomycetes. The so-called stroma of *M. aggregata* is composed primarily of bark cells, evidently altered by the fungal hyphae of the lichen. The blackened area

is first evident with the origin of the ascogonia and gradually expands so as to embrace several perithecia that develop in the same vicinity. The term *pseudostroma* is suggested for structures of this kind.

(4). All species of *Melanotheca* investigated are members of a fairly natural group. Their development is similar to that of *M. aggregata*, and the formation of a pseudostroma seems a character of the genus.

(5). Species assigned to *Trypethelium* are more variable and four types have been differentiated: (1) *T. tropicum* in which the perithecia become superficial and the aggregated perithecia are united merely by coalesced perithecial walls; (2) *T. annulare* in which the perithecia are borne below the surface of the bark without stromoid structures; (3) *T. pallidescens* in which primitive substromata are formed; (4) *T. eluteriae* which forms highly developed substromata.

(6). Species of *Bottaria* and *Tomasellia* investigated possessed pseudostromata; those of *Laurera* possessed substromata.

(7). The Trypetheliaceae cannot be considered a natural group because of transitions between similar forms with and forms without pseudo- and substromata.

(8). The genera that have been placed in the Trypetheliaceae fit much better as terminal members of various series in the Pyrenulaceae.

(9). Some of the lichens with pseudo- and substromata have evolved from lower groups of lichens. They are not merely analogous pseudo- or substromatic Sphaeriales parasitic on species of algae.

(10). The Pyrenulaceae are Ascomycetes and should be considered as such; at the present state of our knowledge they should be classified in the Sphaeriales as a family equal in rank with the Sphaeriaceae and as derived from them.

(11). Cultural records are given for species of *Melanotheca*, *Trypethelium*, and *Laurera*.

(12). Data are presented with reference to the relative abundance of lichen acids in the Pyrenulaceae. These data cor-

relate closely with the suggestions made in this paper with respect to the relationships within the group.

(13). The author is inclined to believe that some of the species studied acquire a portion of their nutrient material saprophytically from their substrata.

(14). The data presented favor the supposition that the first symbiosis in the Pyrenulaceae occurred in relatively recent time with rather advanced fungal components and that the fungi and the lichens (as far as the family is concerned) have evolved concomitantly since that time.

ACKNOWLEDGMENT

The author is indebted to Dr. Carroll W. Dodge for many helpful suggestions, for a portion of the material upon which this study is based, and for the privilege of consulting his private herbarium and library.

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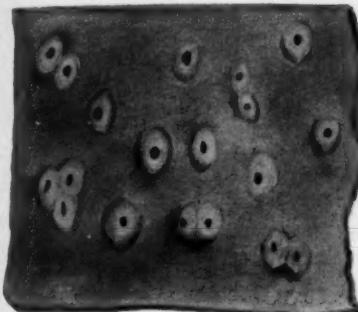
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EXPLANATION OF PLATE

PLATE 1

Habit sketches, illustrating the macroscopic appearance of several pyrenocarpous lichens. These sketches should be compared with photomicrographs of identical or related species which will be found in the other plates. In some cases this plate shows variation in the degree of aggregation of perithecia; in others it suggests how structures differing greatly in microscopic morphology seem similar macroscopically. Miss Elizabeth Heuser assisted in its preparation. (x approx. 12 diameters.)

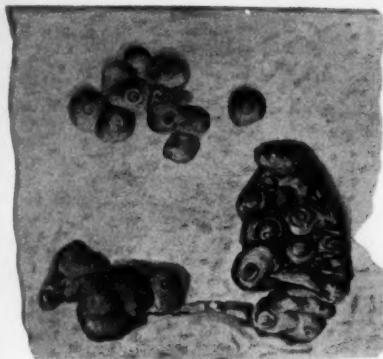
- Fig. 1. *Trypethelium annulare*.
- Fig. 2. *Melanotheca aggregata*.
- Fig. 3. *Laurera madreporfiformis*.
- Fig. 4. *Trypethelium eluteriae*.
- Fig. 5. *Pyrenula mammillana* (Ach.) Trevis.
- Fig. 6. *Trypethelium tropicum*.



1



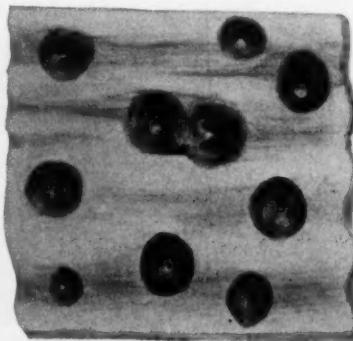
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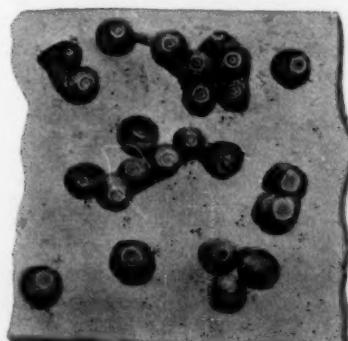
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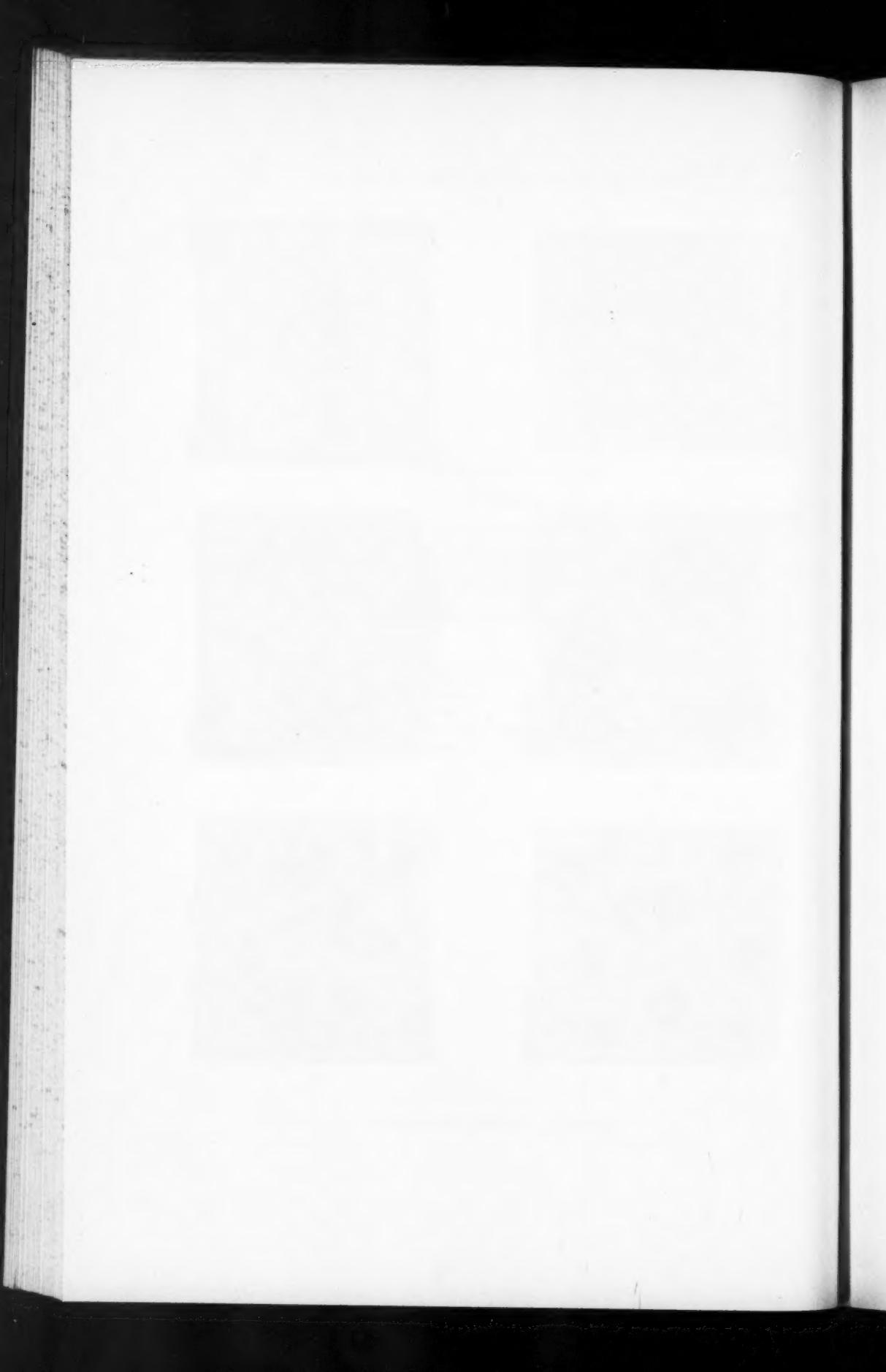


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6

JOHNSON — TRYPETHELIACEAE



EXPLANATION OF PLATE

PLATE 2

Photomicrographs illustrating stages in the development of *Melanotheca aggregata*. (Magnifications approximately as follows: figs. 5 and 6, $\times 60$; fig. 4, $\times 110$; figs. 1 and 7, $\times 200$; figs. 2 and 3, $\times 500$.)

Fig. 1. Two perithecial initials. They are formed a few cell layers below the surface of the bark.

Fig. 2. Young perithecial initial, showing ascogonia.

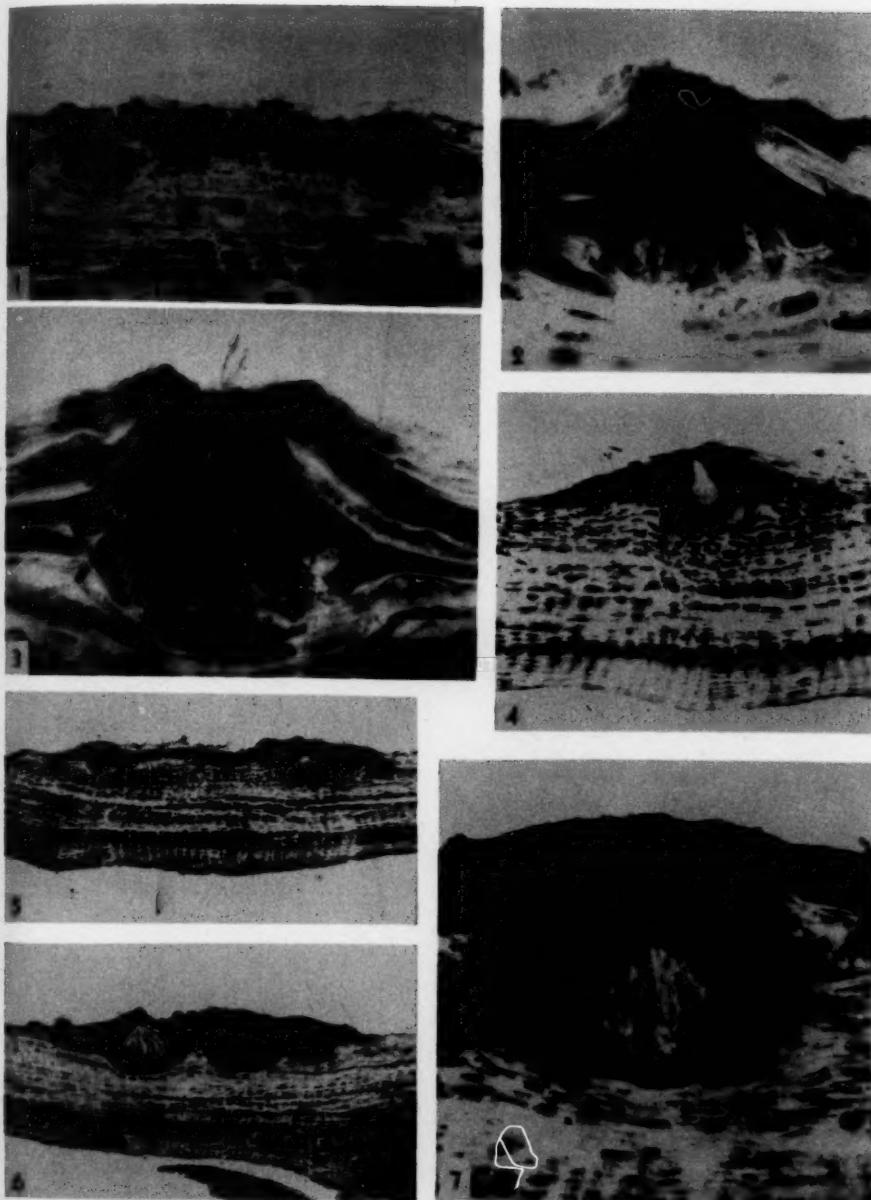
Fig. 3. Perithecial initial, showing ascogonia and trichogynes.

Fig. 4. Peritheciun with a layer of ascogenous hyphae at its base. The "blackened area" which will form the pseudostroma is fairly well developed. This area is quite dense, but its cellular nature is suggested in the lower right-hand portion.

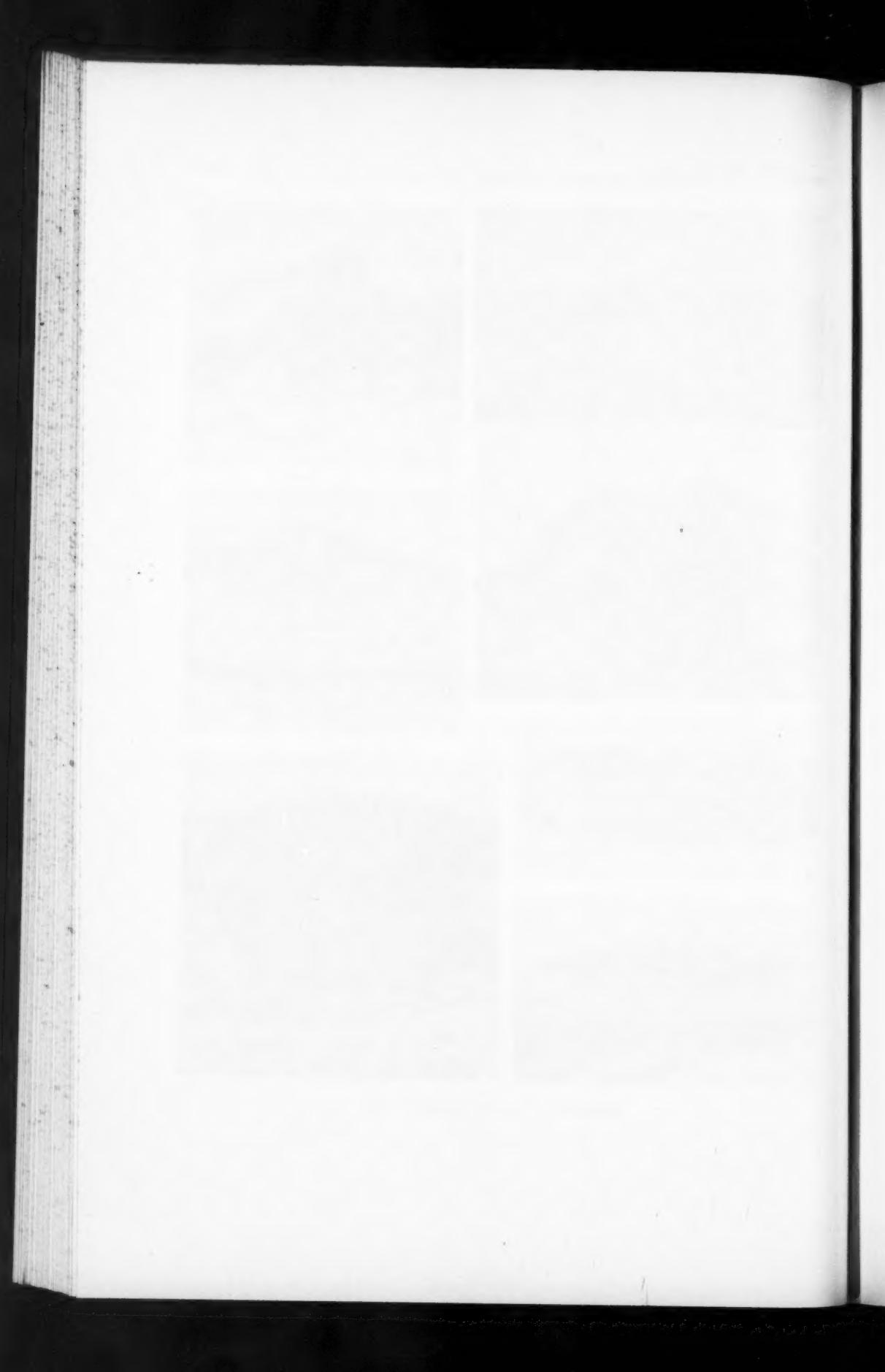
Fig. 5. Early stage in pseudostromatic development. The surface of the bark has become blackened, and this zone encloses several perithecia that have developed in the same vicinity.

Fig. 6. Mature pseudostroma and perithecia.

Fig. 7. Lateral section of a mature peritheciun, showing its relation to the pseudostroma and to unaltered bark cells.



JOHNSON — TRYPETHELIACEAE



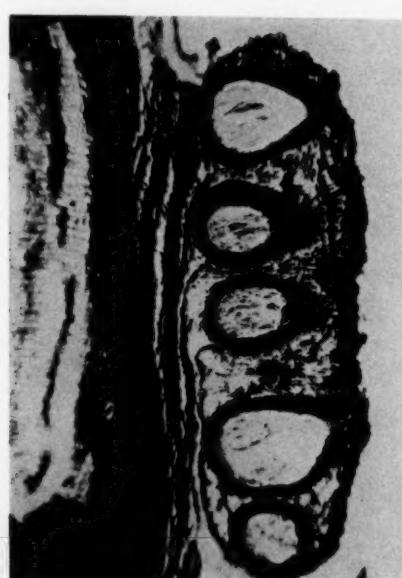
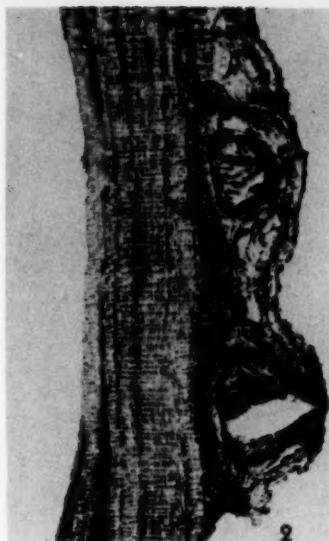
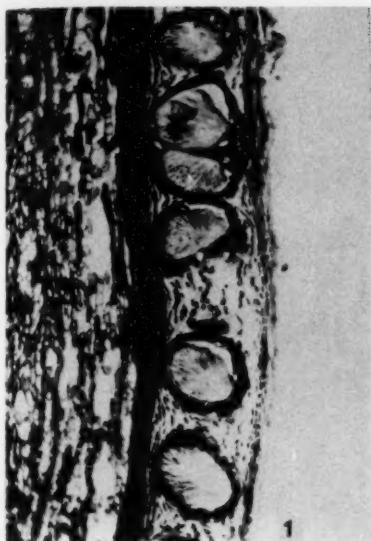


EXPLANATION OF PLATE

PLATE 3

Photomicrographs illustrating the varying microscopic morphology among species that have usually been assigned to the genus *Trypethelium* (x approx. 200 diameters).

- Fig. 1. *Trypethelium pallescens*.
- Fig. 2. *Trypethelium annulare*.
- Fig. 3. *Trypethelium tropicum*.
- Fig. 4. *Trypethelium eluteriae*.



JOHNSON — TRYPETHELIACEAE



EXPLANATION OF PLATE

PLATE 4

Photomicrographs of the vegetative and reproductive structures of various pyrenocarpous lichens (\times approx. 200 diameters).

Fig. 1. *Laurera madreporiformis*. A large number of bark cells are present in the lower portion of the substroma.

Fig. 2. *Laurera chapadensis* Malme. Bark cells surround the perithecial wall.

Fig. 3. *Laurera sanguinaria*. Note the layer of bark cells above the central peritheciun.

Fig. 4. Thallus of *Trypethelium eluteriae*.

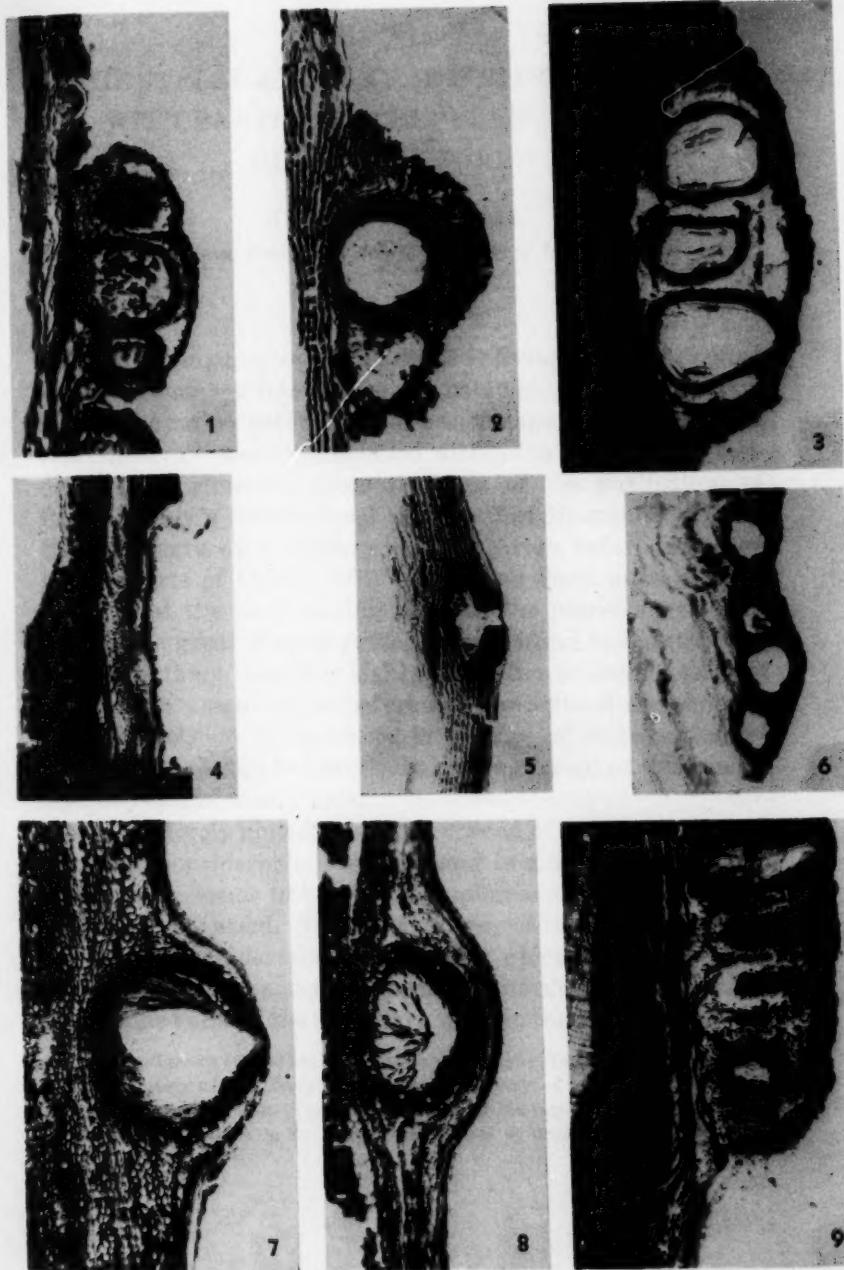
Fig. 5. A species that has been assigned to *Pyrenula*. Several bark cells near the peritheciun have been considerably altered.

Fig. 6. Pseudostroma of *Melanotheca arthonioides*. Its cellular nature is evident opposite one of the lower perithecial cavities.

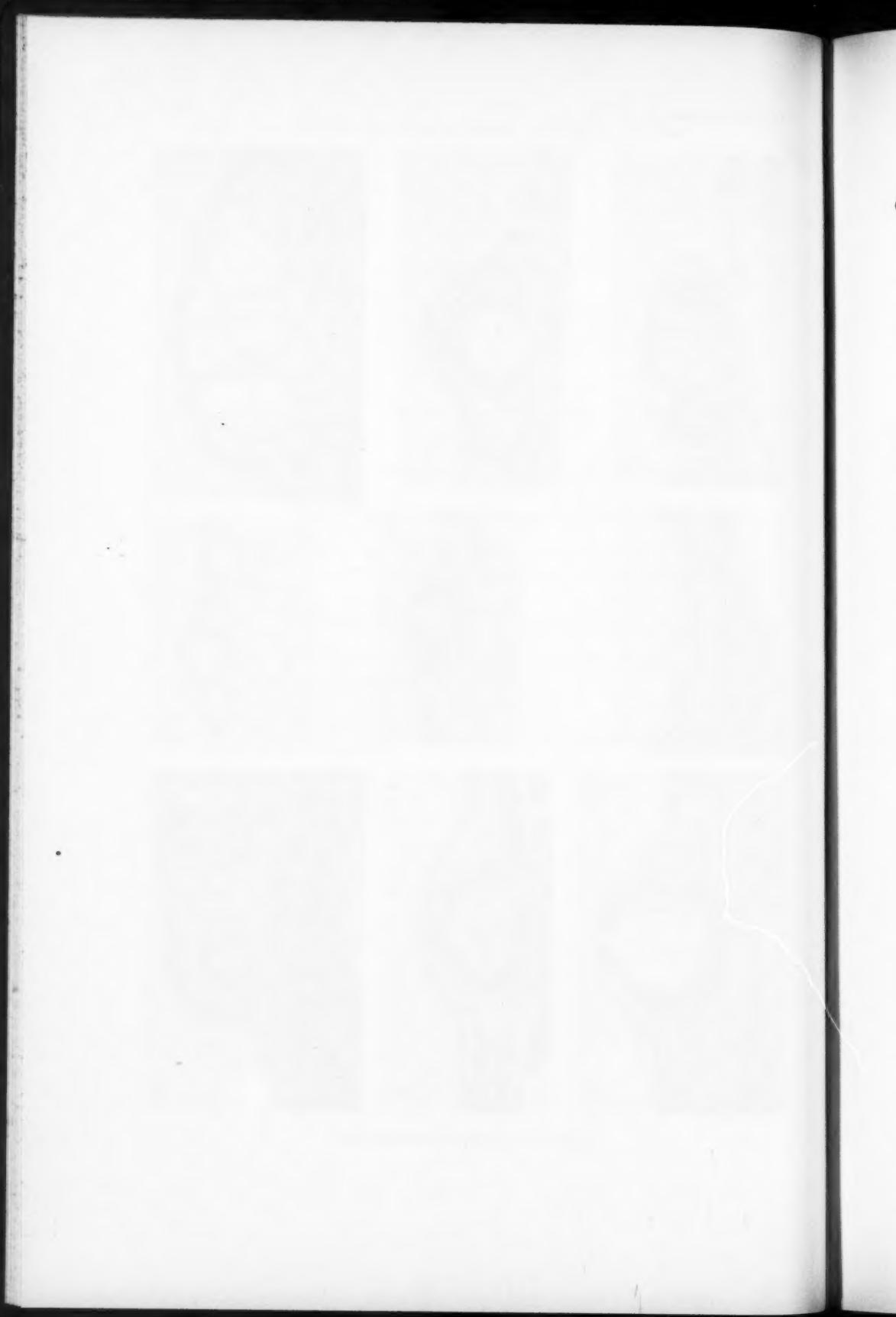
Fig. 7. *Anthracothecium ochraceoflavum*.

Fig. 8. *Anthracothecium pyrenuloides*.

Fig. 9. *Trypethelium eluteriae*. A number of bark cells are visible in the upper portion of the substroma.



JOHNSON — TRYPETHELIACEAE



ON THE STELAR ANATOMY OF THE PTERIDOSPERMS
WITH PARTICULAR REFERENCE TO THE
SECONDARY WOOD¹

HENRY N. ANDREWS, JR.

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INTRODUCTION

Probably no group of plants, fossil or living, has ever created as much combined interest for the botanist, geologist and layman as the rather heterogeneous assemblage of vegetative and reproductive "species" included within the Palaeozoic Pteridospermae. However, from the time of the publication of Palaeobotany's foundational 'Histoire' of Brongniart (1828) three-quarters of a century was to elapse before the combined efforts of Oliver, Williamson, and Scott gave positive evidence of the seed-bearing habit of the pteridosperms, although the great French palaeobotanists had in the previous decades gathered together highly suggestive evidence. An even longer time was to elapse before new concepts of morphology, based largely on an increased knowledge of these and other fossil forms, began to cast doubt on the concept of a filicinean ancestry of the seed plants.

The relatively abundant primary wood of these plants early attracted considerable attention, and in many cases its taxonomic value seems to have been emphasized at the expense of the secondary wood. No careful survey of the secondary wood has ever been undertaken, an omission which is perhaps partly explicable as a reactionary feeling towards the questionable taxonomic value of the secondary wood in certain other groups.

¹An investigation carried out at Cambridge University, England, and in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

The description of many fossil coniferous and angiospermous woods whose affinities are doubtful has tended to discredit the taxonomic value of the secondary wood in general. Only within recent years has a thoroughly organized study of living angiosperm woods been commenced, and already it is proving of great significance.

It is the purpose of this paper to present the results of a study of the secondary wood of many of the plants included within the Pteridospermae and a comparative analysis of the nature and taxonomic significance of the primary and secondary xylem. It is not intended to present an exhaustive treatise on the stelar anatomy of these plants, much of which would only be repetition, but rather to bring to light those aspects of their structure which have been neglected for one reason or another.

Although Harris wrote in 1932 that, "It should be pointed out, however, that we do not know what constitutes a pteridosperm or what are the morphological limits of this class," it will be shown in the following pages that when the supposed seed plants of the Upper Palaeozoic, especially the secondary wood, are studied with reference to their stelar anatomy, three main types may be distinguished. One of them is exemplified by the very simple, mostly protostelic, Upper Devonian and Lower Carboniferous forms (Type I, p. 71); one includes plants of cordaitean-coniferous affinities (Type IV, p. 82); and the third is characteristic of the plants for which the class Pteridospermae was originally established (Types II, p. 72, and III, p. 77).

At the outset it should be stated that the view that the pteridosperms represent an intermediate group between the ferns and the cycads is no longer tenable. Rather we must look to a common psilophytalean-like ancestor with terminally borne sporangia, a solid protostele and primitive secondary wood for the origin of the ferns and pteridosperms (the secondary wood being usually lacking in the former). In support of this view the following points must be kept in mind:

(1) The evidence supplied by fructifications is overwhelmingly in support of the common origin of the ferns and pteridosperms from plants with terminally borne sporangia. This position has been retained by the latter, whereas in the ferns the sporangia have become dorsally located on the leaf-like structures termed sporophylls. There can no longer be any doubt that sporangia had their origin at or near the tips of branches or telomes¹ as evidenced by such plants as *Rhynia*, *Horneophyton* (Barghoorn & Darrah, '38), *Asteroxylon*, *Heidea*, *Sporogenites*, *Psilophyton*, and *Taeniocrada*.²

(2) There is no evidence that the position of sporangia superficially on the dorsal surface of leaves (as in the majority of living ferns) is anything other than derived from a terminal position.

(3) It is only in Upper Carboniferous rocks that fructifications closely comparable with, and which may readily have led to, modern ferns become abundant. Among the better-known forms and their probable relationships are: *Oligocarpia* (Gleicheniaceae), *Seftenbergia* (Schizeaceae), *Ptychocarpus*, *Asterotheca*, and *Scolecopteris* (Marattiales).³

(4) Below the Upper Carboniferous these fern-like fructifications are much less abundant, but, beginning in the Lower Carboniferous rocks and extending up through Jurassic times, there runs quite a different line of microsporangiate fructifications. The fundamental similarity of their organization is such as to indicate with little doubt a great and continuous line of development. Some of the better-known members of this group are: *Telangium*, *Crossotheca*, *Aulacotheca*, *Whittleseyia*, *Potoniea*, *Goldenbergia*, *Dolerotheca*, (Kidston, '23-'25, Halle, '33); *Pteruchus* and *Caytonanthus* (Thomas, '25, '33). The members of this line retained their sporangia in a

¹ With the exception of the Lycopod line represented by such members as *Baragwanathia* and *Protolepidodendron*. In the former the sporangia were borne on the stem close to the leaf axil whereas in the latter they were borne in much the same manner as in *Lepidodendron*.

² A few of the more pertinent publications relating to these genera are: Kräusel ('36), Kidston & Lang ('20-'21), Halle ('36), Dorf ('33), Bertrand ('13).

³ See Kidston, '23-'25; Radforth, '38.

terminal position for the most part, although modified by fusion and aggregation of various types. The plants included under (1) above are undoubtedly representative of the complex from which both the fern and pteridosperm lines arose.

It must be emphasized that there is no evidence that the ferns were evolved prior to the pteridosperms. If either has priority the evidence points rather to the pteridosperms. This is by no means an original concept on the part of the present writer but its significance certainly has been overlooked by botanists in general. Robert Kidston, one of the greatest authorities on Carboniferous floras, presented a concise discussion of the matter in his 'Fossil Plants of the Carboniferous Rocks of Great Britain' (pt. 4, pp. 277-8). He considered in particular the value of the presence or absence of an annulus on a sporangium as a means of distinguishing between ferns and pteridosperms and pointed out that its absence, although generally considered indicative of the pteridosperms, must be used with reserve. Kidston's conclusion, that "They [the ferns and pteridosperms] appear as two distinct groups as far back as they can be traced, and from the earliest time seem to have constituted two parallel lines of development," has been more firmly substantiated since it was written.

It may also be pointed out that the cupule, although a morphologically problematical organ, seems to be a distinctive one of the pteridosperms, and it is now well known from the Lower Carboniferous. This will be discussed further in a later paper.

In view of the above evidence and our knowledge of the actual connection or association of the vegetative and reproductive parts of such plants as *Lyginopteris* and *Heterangium*⁴ and the South African pteridosperms (Thomas, '33), Harris's statement that we do not know what constitutes a pteridosperm is not entirely valid. To be sure, we do not know what the exact limits of the group are but we do have a fair knowledge of the characteristic structures of the types for which it was created, such as the terminally clustered sporan-

⁴See Halle, '29, pp. 18-22, for a summary of known seed-bearing species of pteridosperms.

gia, the cupulate seeds, the fern-like foliage and the secondary wood (see pp. 72-82).

Before presenting the results of the study of the secondary wood the primary body will be considered in the light of Prof. Bower's "Size and Form" principles (Bower, '30). Certainly few greater contributions to morphology have been made in recent years than that author's explanation of the relationship between living parenchyma cells and the dead conductive elements of the primary body. It is safe to assert that had 'Size and Form in Plants' appeared twenty-five years earlier considerably less confidence would have been placed in the taxonomic value of the primary body as a means of delimiting species and genera in the Pteridospermae.

VARIATION IN THE ANATOMY OF THE PRIMARY BODY

Anatomical variations have not gone entirely unnoticed. In 1917 Seward pointed out the fact that:

"The external position of the protoxylem is a character to which too much weight may easily be attached; the difference in position between the protoxylem of *Rhetinangium* and *Heterangium* is in some examples of the latter genus hardly perceptible. Kubart (1914) speaks of the stele of his species *Heterangium Sturi* as being almost exarch. The inconsistency in the position of the protoxylem of the osmundaceous stems and in the primary bundles of *Eristophyton* and other Palaeozoic genera is worthy of consideration in this connexion."

In his discussion of "Old Wood and the New," Scott ('02a) wrote:

"Lastly, we come to *Cordaites* itself, which is anatomically on the same level as recent Cycads; centripetal wood has wholly disappeared from the stem while it still forms the main constituent of the xylem in the bundles of the leaf."

There is, of course, no close relationship between the cycads, on the one hand, and *Cordaites* and related forms, on the other; if such existed in the past it must be traced to a common ancestor in pre-Carboniferous times. Since in practically all of the earliest vascular plants with secondary wood, the centripetal wood composing the metaxylem was abundant if not predominant, its presence in the more conservative parts

of the later divergent groups would necessarily be expected. Like the seed habit, which had its origin independently in various groups such as the cordaites, pteridosperms, and lycopods, the centripetal or "Old Wood" occurs in widely divergent groups and must be used with caution as a taxonomic character. The same holds true for the position of the protoxylem as will be shown in the following pages.

The primary body of Lyginopteris oldhamia (Binney) Potonié

In view of the abundant remains of this plant in Upper Carboniferous times, its wide distribution, and the many authors through whose hands it has passed, a further consideration may seem superfluous. Although the great range in size and structural details of the stem particularly is generally known, the figures and descriptions are scattered through the literature and many of the more interesting features have never been adequately described. Furthermore, it is only when such figures are presented at the same magnification that a true picture of the variation is realized.

Figures 1 to 10 of plates 5 and 6 represent transverse sections (all shown at a magnification of $\times 7.5$) which have been selected to show variation in size of the stem, the nature of the primary xylem, and the sclerotic "nests" and resin cells.⁵

The limits of publication necessitate the presentation of only the most outstanding features. It must be borne in mind, however, that one of the most significant points in the stelar variation of *Lyginopteris* lies in the fact that no sharp divisions can be drawn separating true forms or varieties. The variation is wide but the almost inseparable intergradations preclude any segregation.

a. Size variation.—The great variation in the size of the primary body of the stems may be seen by comparing figs. 1 and 2 of pl. 5. Although I have observed but few stems smaller than that shown in fig. 2 the larger one shown in fig. 1 is not

⁵ These have been drawn from a study of some few hundreds of slides of this plant contained in the Scott, Williamson, Kidston, Manchester, University College (London), Binney (Cambridge), Cambridge Botany School, and Liège University Collections, in addition to numerous "nitrocellulose pull" preparations and blocks, supplied to the author by Messrs. W. Hemingway and J. R. Lomax.

the maximum that the stems may attain. Aside from its somewhat exceptional size, fig. 1 represents a more or less typical stem with respect to relative extent of primary and secondary bodies, abundance and distribution of primary xylem, and sclerotic "nests." It is quite similar to the type specimen (pl. 6, fig. 5) except that the primary body of the latter is relatively smaller.

b. Parenchyma-sclerenchyma relationship.—There is considerable divergence from the more or less spherical nests as seen in figs. 1 and 5. In addition to such groups there are usually scattered through the pith numerous individual cells (sclerotic or resinous) with dark contents. In some sections the sclerotic nests are absent and the individual secretory cells are more or less uniformly scattered throughout the pith (fig. 4). Particularly small stems (fig. 2) may be almost or entirely lacking in either. That fig. 2 represents a small but mature stem and not merely a young one is evidenced by the prolific secondary xylem.

The distribution and abundance of these pith elements may be highly variable. In figs. 1 and 4 they are quite uniformly distributed, whereas in fig. 8 they form a peripheral cylinder immediately within the secondary xylem, or they may be confined to the central region of the pith as in fig. 7 and to a lesser extent in fig. 10.

c. Primary xylem.—The primary wood, with its mostly centripetally developed elements, generally occurs as five or six rather widely separated eccentrically mesarch bundles in direct connection with the secondary wood. However, the occurrence of a continuous band of primary tracheids in small stems (fig. 3) or of a nearly continuous ring in larger stems (fig. 9) is not uncommon. Various intermediate forms between continuous rings and typically scattered bundles (figs. 1, 5) are to be found. In pl. 8, fig. 17, the primary xylem extends unbroken through approximately 180° , the remainder of the periphery being composed of isolated bundles.

The eccentrically mesarch bundles are well known and need no further description here, but a few of the more interesting

divergences from the normal bundle (shown for comparison in pl. 10, fig. 32) may be briefly noted. Figure 35, a camera-lucida drawing of a bundle in the stem shown in fig. 17, shows abnormally high development of the centripetal elements. Figure 34 shows a very loosely aggregated "bundle" with no readily distinguishable protoxylem. The nature of the specimen whose primary bundle is shown in fig. 35 will be taken up below.

d. Extra-stelar meristematic activity.—The most remarkable stem referable to *Lyginopteris oldhamia* that has come to my attention and which, to my knowledge, has never been described is shown in pl. 7, figs. 11, 14, 15, 16; pl. 10, fig. 33. Its extraordinary feature lies in the presence of a complete medullary cylinder of secondary xylem.

The occurrence in *Lyginopteris* of internal (secondary) xylem in association with the primary bundles (fig. 12) and even irregularly scattered between them (fig. 13) is not uncommon, and as such may be of no phylogenetic significance; at least such was the opinion of Williamson and Scott (1896). But when this internal xylem forms a complete cylinder it most certainly merits careful consideration. The tracheidal cells of this internal secondary xylem are arranged for the most part in radial rows and are of about the same size as the earliest formed centrifugal secondary xylem tracheids; the degree of lignification is the same in both. The amount of associated "ray" or parenchyma cells may be seen to be somewhat greater in the former.

The nature of the tissue between these two bands of secondary xylem is shown in figs. 16 and 33, the latter being a camera-lucida drawing. It will be noticed that there is a striking resemblance to the "partialmark mit primartracheiden" of the Chemnitz Medullosas (Weber and Sterzel, 1896). No distinct primary bundles are present, the primary tracheids being scattered as individual cells or in small groups throughout the "partialmark." When in small groups they are usually in contact with the tracheids of the normal secondary xylem (fig. 33), but the groups consist of only a few cells and lack a distinct protoxylem.

The ontogenetic origin of such an internal cylinder of xylem is of considerable interest. If it had been laid down in the usual way for secondary wood, by a single row of meristematic cells, one would expect the parenchyma, either on its inner or outer face, to show some indication of crushing. It is, however, for the most part well preserved and there seems to have been no crushing.

Another type of meristematic activity which occasionally occurs in *Lyginopteris* stems may be noted. At *a* in pl. 8, fig. 19, a group of radially arranged cells appears which are almost in contact with the normal secondary xylem and tend to flare out somewhat at the opposite extremity. The cells of such groups are not always radially arranged but may be less regularly oriented as shown in fig. 13. They are unlignified and there is no indication of a true cambium. Whether or not the internal secondary xylem described above represents a later stage (after lignification) cannot be proven but presents an interesting possibility.

It is evident from Miss Esau's studies that the sharp distinction between primary and secondary vascular tissues on the basis of radial arrangement is invalid. She has shown that in *Nicotiana glauca* Graham and *N. tabacum* L. ('38) and in *Apium graveolens* L. ('36) the procambium may lay down radial rows of primary xylem. Of the latter species she states:

"As the layer of dividing procambium cells narrows down to a few rows of cells, the meristem shows an increasing similarity to the cambium of herbaceous dicotyledons. Eventually cells appear with short radial diameters and become arranged, in longitudinal sections, in horizontal tiers. The longitudinal divisions are predominantly perielinal and the resulting cells retain a radial arrangement in the mature state." ['36.]

Since the ontogeny of primary and secondary vascular tissues is a continuous process (except where the primary xylem is entirely centripetal) one must follow Miss Esau's conception of procambium and cambium as two developmental stages rather than as two distinct meristems. In the light of our knowledge of such procambial activity in living plants it appears not impossible that this apparently secondary centripetal growth in *Lyginopteris* may be of like origin.

Williamson and Scott (1896) dismissed these anomalies as lacking significance and in his 'Studies' (1923) Scott writes:

"The most frequent anomaly in *L. oldhamia* is the formation of a medullary cambium, usually arising first inside the primary xylem strands and producing wood and bast with inverted orientation. . . . in extreme instances the wood may become broken up into several distinct masses, each with its own ring of cambium, forming new secondary tissues all around it."

The conclusions of these authors might be accepted without reservation for instances where the internal xylem is associated only with leaf traces (pl. 7, fig. 12), but when it forms a complete ring the similarity to such woods as *Cycadoxylon robustum* or certain of the Permian Medullosas is too striking to ignore any possible phyletic implications.

Although the identification of the specimen may be called into question, there seems to be sufficient evidence in favor of its allocation to *L. oldhamia*. Most of the tissues external to the secondary xylem have been destroyed, although there is a fragment of the characteristic "Dictyoxylon" cortex present. The characteristic sclerotic nests and secretory cells are present in the pith (pl. 7, fig. 11), and the general structure of the centrifugal secondary xylem is typical. Furthermore, this internal secondary xylem occurs in association with leaf traces (fig. 12) and even irregularly scattered between them (fig. 13) in undoubted specimens of *L. oldhamia*.

e. Roots.—The relationship between the tracheids and parenchyma in the roots of *L. oldhamia* in general coincides with the physiological requirements of Bower's "Size and Form" principles. The smaller roots (pl. 8, fig. 22) usually have a solid primary body while in the larger (figs. 20, 21, 23) there is an admixture of parenchyma (these figures are all at a uniform magnification of $\times 23$). The root shown in fig. 22 is about the maximum size that the primary body may attain and still remain purely tracheidal. All roots smaller than this that have come to my attention are likewise composed of tracheids only. When, in the larger roots (figs. 21, 23), the primary body contains an appreciable amount of parenchyma the xylem is broken up into rather regular groups with the protoxylem

outermost; and when the tracheids largely disappear from the central region the roots may present a striking resemblance to the stems (figs. 9 and 20).

f. Foliage.—It has been pointed out in the preceding paragraphs that, although these plants have a wide range of variation in the primary body they form a continuous series. Such is not the case with the foliage "species" associated or in organic connection with the stem remains.* The frond species, on the contrary, are distinct and appear to present a significant example of the varying rate of evolution that different organs undergo.

Sphenopteris Hoeninghausi Brongniart is so well known and has been found so often in contact with the stems having a *dictyoxyllic* cortex that it needs no further mention here. It is, however, not so well known that *Sphenopteris Baumleri* Andrae has been found in organic connection with stems exhibiting the *dictyoxyllic* cortex. Although Gothan ('23), Kidston ('23-'25) and Stur (1885) have figured this it does not seem to have attracted the attention that it merits. While I was studying in Bruxelles, Dr. Stockmans showed me two fine specimens from the Westphalien of Belgium (Nos. 5933, 5930, Mus. d'Hist. Nat., Brux.) in which *S. Baumleri* was associated with the *dictyoxyllic* stems. In the latter specimen (No. 5930) the similarity between the stem compressions associated with *S. Baumleri* and those to which *S. Hoeninghausi* is attached (*Lyginopteris*) extends beyond that exhibited by the hypodermal sclerenchyma, for numerous spines are to be observed quite like those found on the rachis of *S. Hoeninghausi*.

In addition to these two well-defined species of *Sphenopteris* actually in organic connection with the *dictyoxyllic* (*Lygi-*

* Lacking the evidence of internal structure the only characters on which the supposed identity of *Lyginopteris oldhamia* stems is based are the anastomosing strands of hard cortical tissue and in some cases the presence of epidermal spines. Considering the wide distribution and abundance of *L. oldhamia* stem petrifications it is likely that many of the stem and petiole compressions exhibiting a "Dictyoxylon," or perhaps better a *dictyoxyllic* cortex, actually do belong to that species; nevertheless they cannot be proven as such. Paleobotanists have perhaps accepted this external evidence a bit too freely.

nopteris type) stem, others are found in association. A specimen of *S. taitiana* Kidston from the Vendéenne region in France has been figured by Mathieu ('37, II, pl. 7, fig. 6) in association with a fragment of a rachis (or stem?) showing cortical structure characteristic of *Lyginopteris*. Zeiller (1897) described a specimen of *Diplotmena distans* (Sternberg) Stur which, judging from the account, must have been attached to a stem of the dictyoxyllic type:

"Quant à l'axe principal, sa surface est divisée en compartiments fusiformes inégaux et irréguliers, de 4 à 6 millimètres de longueur, circonscrits par des stries longitudinales flexueuses entre-croisées, qui donnent lieu de penser que l'écorce était formée, au voisinage de sa surface externe, de bandes sinuées résistantes, comprenant entre elles des mailles de tissu plus mou. C'est ce que a lieu dans les écorces du type connu sous le nom de *Dictyoxylon*, où des mailles parenchymateuses sont ainsi encadrées entre des bandes sinuées de sclérenchyme, organisation que Williamson a reconnue notamment chez son *Lyginodendron Oldhamium*.

"Ainsi constitués, ces larges axes charbonneux ressemblent d'une façon frappante à ceux qu'on observe chez le *Sphenopteris Hoeninghausi* Brongt. . . ."

The petioles described under the name of *Lyginorachis* likewise present a range in anatomical variation similar to that in the gross external morphology of the fronds. In addition to the petioles of *Lyginopteris oldhamia* five other species of petiole (*Lyginorachis*), for the most part well defined, have been described, namely, *L. taitiana* Kidst. & Crookall, *L. papilio* Kidst. & Scott, *L. Waltoni* Calder, *L. Brownii* Calder, and *L. sp.* (Crookall, R., '31).

Summarizing briefly, it may be seen that the stem anatomy, although highly variable, forms a nearly continuous series, whereas the foliage and petioles, for the most part, represent well-defined species. *Sphenopteris Hoeninghausi* is somewhat of an exception to this in that it is difficult to distinguish from other very closely allied species. Seward in 1917 noted that:

"It is not an easy task even for those most familiar with Carboniferous fronds to distinguish clearly between species agreeing generally with *Sphenopteris Hoeninghausi*, a species regarded by some authors as the type of a group of very similar and closely allied forms all of which were probably borne on stems referable to the genus *Lyginopteris*."

The Calamopityeae

Of all the supposed pteridosperms preserved as petrified stem remains the assemblage included under the *Calamopityeae* presents the most difficult taxonomic problems, as is adequately attested by the frequent revisions of members retained within the group.

Calamopitys saturni Unger and *C. annularis* (Unger) Solms are the oldest known members of the *Calamopityeae* as instituted by Solms-Laubach in 1896, the former species being the genotype. A few years later Scott (1902) described two more species of *Calamopitys* (*C. fascicularis* Scott and *C. beinertiana* Scott) after having tentatively assigned them in a previous publication (1899) to *Araucarioxylon*. Zalessky ('11) in turn proposed the genus *Eristophyton* to include these latter two which differ very markedly from either *C. saturni* or *C. annularis* in the structure of the secondary wood and in the structure and arrangement of the primary bundles. Read ('37) has upheld Zalessky's genus and there can be little doubt that this decision is correct. It is, moreover, doubtful whether the very problematical *Calamopitys radiata* Scott, with its highly dilated rays, should remain in the genus. Lastly it may be noted that *Sphenoxyylon eupunctata* (D. E. Thomas) Read, originally described as a *Calamopitys*, agrees neither in the nature of its primary or secondary wood with *C. saturni* or *C. annularis*. There can be little doubt that it is generically distinct and for that reason the name *Sphenoxyylon* proposed by Read ('37, p. 91) is adopted here.

Judging from the wide divergence of characters in the members of the *Calamopityeae*, the family can hardly be considered a natural group, as it stands at present. Two points are particularly significant in the history of the group, namely, the early recognition of the similarity of *Calamopitys* (i.e., *C. saturni* and *C. annularis*) to *Lyginopteris*, and Scott's original description under *Araucarioxylon* of the species at present retained in the genus *Eristophyton*.

The close similarity, if not actual identity, of *Calamopitys americana* Scott & Jeffrey, *C. saturni* Unger, and *C. annularis*

(Unger) Solms is well known to those who have dealt with the group. The differences between *C. americana* and *C. annularis* are exceedingly slight, while *C. saturni* is supposed to be unlike these two in having distinctly separate centrally mesarch strands and a primary xylem consisting of a nearly confluent ring with eccentric protoxylem.

Through the kindness of Professor Gothan a considerable number of the type slides of *C. annularis* was obtained from Berlin.⁷ They apparently were not seen by Scott at the time he wrote his "Notes on *Calamopitys* Unger" ('18), since the slides he observed are still in the Scott Collection under the numbers 3676-3681 inclusive.

In the American species, *C. americana*, the primary body is described by Scott and Jeffrey ('14) as follows: "So far the primary structure—pith surrounded by a ring of nearly confluent mesarch xylem strands—is quite similar to that described in the case of *Calamopitys annularis*. In the American species, however, there is strong evidence for the somewhat unexpected conclusion that the pith was a 'mixed' one, containing tracheids." Read ('37) has confirmed the existence of a mixed pith in this plant.

In 1918 Scott notes with regard to the possible presence of medullary tracheids in *C. annularis*: "I have carefully looked into this question. In transverse sections one can distinguish at a few places elements with thicker walls than the ordinary parenchyma, and resembling the tracheids of the xylem ring. But the preservation is not such as to make these indications at all convincing." Now the slides 97(40a) and 101(43I), not

⁷ The slides from Berlin examined by the writer are as follows (the numbers and notations given as they appear on the slides): RADIAL SECTIONS: 97(40R) *Calamop. ann.* Berlin Landesanst; 101(44R) *C. annul.* Culm, Saalfeld, Berlin Landesanst; 49(6R) *Calamop. annular.*, Culm, Saalfeld, Berlin Landesanst; 101(44) *Stigmaria annularis*, Saalfeld, Berlin Landesanst; 49(6R) *Calamop. annularis*, Berlin Landesanst; 100(43I) *Stigmaria annul.* Saalfeld, Berlin Landesanst; 49(6R) *Cal. annul.* Berlin Landesanst; 101(44) *S. annul.* Culm, Saalfeld, Berlin Landesanst. TRANSVERSE SECTIONS: 97(40a) *Calam. ann.* Berlin Landesanst; 74(24) *Stigmaria annul.* Saalfeld, Richt., Berlin Landesanst; 98(41) *Stigmaria annularis*, Saalfeld, Richter, Berl. Landesanst; 100(43I) *Stig. annul.* Saalfeld Richter, Berlin Landesanst. TANGENTIAL SECTIONS: 49(tg) *Calamop. annul.* Culm, Saalfeld, Berlin Landesanst.

seen by Scott, are very well preserved, and I believe there can be no doubt that the pith is mixed, that is, with tracheids scattered through it. Judging from a careful comparison of the slides of *C. americana* and *C. annularis* in the Scott and Berlin collections there seems to be no valid reason for the existence of two species based on this material.

The differences between *C. annularis* (or *C. americana*) and *C. saturni* are primarily the presence of a discontinuous xylem ring in the primary body of the latter and the position of the protoxylem. The primary body is comparatively large in the first two species (7 mm. or more as compared with less than 2 mm. in *C. saturni*), but in view of the size difference in other species of pteridosperms as shown here and the host of plants considered by Bower ('30), that alone can bear little weight. In the Berlin slides 97(40a) and 100(43I) of *C. annularis* primary xylem does not form distinctly continuous rings (pl. 9, fig. 29); at least the variation from a continuous ring is of sufficient significance as regards the supposed distinction of these species.

Perhaps the most interesting slide of all those received from Prof. Gothan is No. 74(24), labeled *Calamopitys annularis*. It is quite likely that it was cut from the same specimen as the section described by Scott ('18, p. 214) which he tentatively assigned to *C. annularis*. Since it has a distinct bearing on the taxonomy of these three species and is better preserved than the slide described by Scott, a detailed description will be given.

The distinctive features in the slide at Scott's disposal may be briefly summarized as follows: primary body only 2.5×1.7 mm.; primary xylem forms a continuous band, while elsewhere there are only scattered tracheids between the primary strands; position of protoxylem not determined; rays of secondary wood narrow.

In my slide the nature of the primary body may be seen in pl. 8, fig. 18, pl. 9, fig. 30. The primary xylem resembles that in the Scott slide but is better preserved, the protoxylem elements being centrally mesarch in most of the bundles—a dis-

tinctive feature of *C. saturni*. It may be noted, however, that in the two bundles shown in fig. 18 the position of the protoxylem varies, that in the bundle at *a* being eccentric. On the other hand, the xylem forms a nearly continuous ring, that part of the primary body between the bundles proper being occupied by tracheids with a few admixed parenchyma cells. There are, however, scattered tracheids within this ring—a feature of *C. americana* and *C. annularis*.

In view of this admixture of characters, it is evident that the distinction between the three "species" is not sharp. A feature of their leaf-trace anatomy may be noted. In slide 3680 (apparently cut from the same block as Berlin slide 98(41)) Scott ('18) described two complete bundles in the cortex or leaf base: "Each is elongated, approximately in the radial plane, and has three internal protoxylem groups, the latter lying toward that side of the strand which faces its neighbor." In the Berlin slide, however, there are four instead of three protoxylem groups in one of the strands, and their position is eccentric towards the outside rather than on the side adjacent to the other strand. It appears then that as the traces pass out not only does the number of the protoxylem groups change but also their position. This is not surprising in view of the sudden change that may take place in the nature of the vascular supply of many living plants—any one who has taken the trouble to follow the course of the bundles in the basal portion of the petiole of such a plant as *Aesculus Hippocastanum* L. could not fail to be struck by the rapid change through a few millimeters. Such rapid ontogenetic changes give a hint of the caution that must be used in comparing supposedly different fossil species unless equal parts of homologous structures be available for comparison.

Although perhaps these three species of *Calamopitys* should not be merged until further material is obtained, in view of the variable nature of the primary body in this and other groups, combined with the modern concepts of "Size and Form," the specific distinctions are questionable. An investigator of the present day would certainly describe them as variant of a single species.

Eristophyton Beinertianum (Goeppert) Zalessky and *E. fasciculare* (Scott) Zalessky present certain points of interest which are appropriate to the present discussion. In both species the protoxylem of the leaf-trace bundles, although mesarch at the point of entrance, becomes endarch as it passes down the stem. A further instance of the variation that may be expected in size of the primary body is found in *E. Beinertianum*. First, it may be recalled that the diameter of the primary body of the British specimens varies from 13 to 15 mm., while it is 8 mm. in the Falkenberg specimen (Scott, '18). There are, moreover, four uncatalogued slides in the Scott Collection labeled "*Calamopitys*, Gin Head Vent, near Tantallon Castle, North Berwick." The primary xylem is poorly preserved but in all four the sclerotic "nests" characteristic of *E. Beinertianum* are prominent, and the general appearance of the secondary wood leaves little doubt as to their identity. The dimensions of the primary body and the total diameter (nothing outside of the secondary wood is preserved) of the stems in these four slides are given in table I.

TABLE I
EXPLANATION IN TEXT. ALL DIMENSIONS IN mm.

Slide No.	Primary body	Diameter over all
1	9 x 14	27 x 35
2	4	20
3	3.5	11
4	5	22 x 18

Endoxylon zonatum (Kidston) Scott was segregated from *Calamopitys* (Scott, '24a) primarily on the basis of its endarch primary xylem strands. An examination of the sections in the Kidston Collection has convinced me that this feature is not constant. In slide 803 Kidst. Coll., a strand may be noted that is more mesarch than endarch.

To emphasize further the necessity of caution in the taxonomic use of characters of the primary body a few examples of plants not included within the Pteridospermae may be mentioned.

Although the slides of *Mesopitys Tchihatcheffi* (Goeppert) Zalessky were not available for my examination, Seward's opinion ('17) is of interest: "I am not convinced that the primary xylem-strands are exclusively endarch; in most of the primary groups the protoxylem is clearly on the inner edge, but in a few cases there may be a small amount of centripetal xylem present."

Certainly one of the most remarkable cases of ontogenetic variation in the primary body is that of *Selaginella spinulosa*. Here, according to Gibson (1894), in the upper region of the erect stem seven protoxylem strands occur on the outside of the stele. Farther down these fuse to form three (still exarch), and in their course down the stem they gradually pass toward the center of the stele until, in the trailing axis, they fuse to form a single central protoxylem strand. Not only does the number of protoxylem groups change but there is a complete transition from centrally endarch in the trailing axis to exarch in the stem.

A fine example of the physiological relationship between primary tracheids and parenchyma is shown in the famous fossil hollow trees of Aran, *Lepidophloios Wunschianum* Carruthers. Although it had long been supposed that the steles of other plants had washed into the rotted hollow centers of the trunks, Walton ('35) showed that as the small solid primary xylem enlarged upward the degree of medullation correspondingly increased.

ANATOMY OF THE SECONDARY WOOD

As was pointed out in the introduction, a careful consideration of the characters afforded by the secondary xylem presents an outstanding gap in the literature, particularly in the light of current studies of dicotyledonous woods. This is well illustrated by the original description of *Megaxylon* in which the secondary wood was described as practically identical with *Cycadoxylon (Lyginodendron) robustum*. The latter has also been compared closely with *Lyginopteris oldhamia* (Scott, '23). However, if the ray structure of these three be compared

(pl. 13, figs. 39, 40; pl. 14, fig. 42) all three are found to be distinctive.

The secondary xylem in the pteridosperms has been studied in detail to determine what characters, if any, are sufficiently constant to be relied on.

Materials and Methods.—The author has been fortunate in having had access to the type slides of the majority of the pteridosperm woods discussed below, and in many cases the type specimens or additional blocks have been available. The specimens thus dealt with are:

Cycadoxylon robustum (Seward) Scott: portion of the type block from the British Museum (Natural History).

Cycadoxylon anomalum (Will.) Will. & Scott: portion of the type block from the Hunterian Museum, Glasgow University, Glasgow.

Megaloxylon Scotti Seward: portion of the type block from the Binney Collection, Sedgewick Museum, Cambridge.

Lyginopteris oldhamia (Binney) Potonié: numerous blocks supplied by W. Hemingway (Derby) and J. R. Lomax (Bolton); a block from the Binney Collection, Sedgewick Museum, Cambridge.

Medullosa anglica Scott: block supplied by J. R. Lomax.

Medullosa Noei Steidtmann: blocks in the Botany School, Cambridge; blocks supplied by Dr. James Schopf, Illinois State Geological Survey.

Medullosa stellata Cotta, *M. Solmsii* Schenk, *M. Leuckarti* Solms-Laubach: blocks deposited in the Botany School, Cambridge.

Heterangium sp.: block supplied by Prof. W. T. Gordon, King's College, London.

Where the preservation has been particularly good serial tangential sections have been prepared through the secondary wood, using the cellulose-pull technique; when the wood was not sufficiently well preserved to permit this technique ground sections were cut as close together as possible.

The anatomy of the secondary xylem was investigated first to determine whether or not the ray structure is constant

throughout the radius and whether it could be correlated with other characters such as pitting and tracheidal morphology. Since the ray structure presents the most reliable taxonomic character of the secondary wood, the ray types into which most of the pteridosperm woods may be segregated will be described and illustrated. The blocks were in varying states of preservation and in one group the rays were extremely tall. For these reasons uniformly good photographs could not be obtained and drawings were prepared by means of a reflector attached to a vertical photomicrographic camera.

It is not possible to classify these woods on the basis of their ray structure according to the system employed for angiosperm wood by Kribs ('35). Until more extensive studies are made of other groups it seems best to set up an independent classification for the plants discussed here. Four rather distinct ray types are found within the group:

- I. Rays varying from very low (3-4 cells) and uniseriate to tall (usually not over 2 mm.) and 3-4-seriate, the latter not regularly fusiform, heterogeneous. (Chief feature is the uniform gradation between low uniseriate and rather tall irregularly multiseriate). Pl. 12, fig. 37.
Sphenoxyylon, Tetrastichia, Palaeopitys, Aneurophyton.
- II. Rays of great height, up to and exceeding 2 cm.; sides generally parallel but occasionally irregularly dilated; low uniseriate or fusiform rays extremely rare; cell walls very thin, mostly unpitted; cells angular, heterogeneous, intercellular spaces small.
 - A. Rays of first-formed secondary xylem usually narrow, becoming greatly dilated toward the outside. Pl. 14, fig. 42.*Lyginopteris.*
 - B. Similar to A but less variable in tangential dimensions, usually not more than 4-5 cells wide. Pl. 12, fig. 38; pl. 14, fig. 41.*Heterangium, Stenomylon, Calamopitys, Ehotinangium, Sutcliffia, Megaloxylon, Medullosa* (in part)—*M. anglica, M. Noei, M. pusilla, M. centrofisia, M. distelica, M. Leuckarti.*
- III. Rays elongate-fusiform to nearly circular (that is, with tangential and vertical dimensions nearly equal), heterogeneous, uniseriate rays rare. Pl. 11, fig. 36; pl. 13, fig. 39.
Cycadoxylon, Colpoxyylon, Ptychoxylon, Medullosa (in part)—*M. Solmsi, M. gigas, M. stellata* (?)
- IV. Rays mostly uniseriate, occasionally 2-4-seriate, low, generally not more than 7-10 cells high; heterogeneous; cell walls relatively thicker than in other groups. Pl. 15, figs. 43, 44.
Eristophyton, Bilignea, Protopitys, Cladoxylon, Endoxylon.

TYPE I.

Type I is illustrated by a camera-lucida sketch (fig. 37) from slide 15T6 Petry Collection (Cornell U.). It is a partial reconstruction in the sense that it represents a composite view of a number of the best-preserved portions of the slide. Other slides were available and as the preservation of the stele of this plant is in general very good the drawing is an accurate generalized reproduction of the ray structure. The secondary woods of *Palaeopitys* and *Tetrastichia* are not as well preserved, particularly the former. However, a careful examination of the slides in the Kidston and Gordon Collections indicates that their ray structure is essentially the same as that of *Sphenoxylon*. Although slides of *Aneurophyton* have not been available for examination, the description given by Kräusel ('36) indicates a close similarity to the other members of this group. Because these early forms are of particular interest as possible forerunners of the Pteridospermae proper a brief summary of the structure of their primary body is included here:⁸

*Although the present treatise involves primarily the stelar anatomy of the pteridosperms, a discussion of the seed or megasporangiate fructifications should be appended in order to present a composite picture of these very early Gymnosperms or "Pro-Gymnosperms." The latter term, originally introduced by Saporta and Marion (1885) to include plants of sigillarian, calamarian, and cordaitean affinities, or the term Hemi-Gymnosperm, is probably more truly descriptive of the plants included under Type I than any other. On the basis of anatomy alone this may appear too speculative but when considered in the light of the fructifications discovered in recent years in these correspondingly early rocks such a belief seems justified. The morphology of the secondary enclosing structure, the cupule, of certain Lower Carboniferous seeds is indeed a pressing problem. Recently an extraordinary large cupule (6.2 cm. long) was discovered in the Lower Carboniferous oil shales of Scotland and will be described in a separate paper. This cupule, as well as *Calathiope Bernhardti* Benson, probably contained in life more than one seed, whereas the smaller forms, such as *Calymmatotheca Kidstoni* Calder (Calder, '38), contained only one seed as in the Upper Carboniferous ones.

In his discussion of the affinities of that extremely interesting plant *Tetrastichia bupatides*, Gordon ('38) has pointed out certain similarities with the petiole base of *Telangium affine*, and it may also be noted that the only foliage (other than that of Lycopods) found in association with the above-mentioned cupule is again *Telangium affine*. The evidence of association is highly suggestive.

Palaeopitys Milleri M'Nab (Kidston & Lang, '23). Solid protostele 1.5 mm. in diameter, protoxylem elements probably near secondary wood. Mid-Devonian.

Aneurophyton germanicum Kräusel & Weyland (Kräusel, '36). Solid protostele, approximately 1.5-3 mm. in diameter, triarch, the three protoxylem groups near the periphery. Mid-Devonian.

Tetrastichia bupatides Gordon (Gordon, '38). Solid 4- or 5-rayed protostele 1.5-2.5 mm. in diameter, with protoxylem centrally placed in the arms. Lower Carboniferous.

Sphenoxyylon eupunctata (D. E. Thomas) Read (D. E. Thomas, '35). Primary body consisting of medullated central column 4×2 mm., with four radiating arms of primary xylem. Upper Devonian.

It is of interest to note that the primary body in three of these four genera is a solid protostele. In *Sphenoxyylon*, with its somewhat larger primary body, it is not surprising to find it mixed. Bower has shown that in the Psilotales and Psilophytales the increasing size of a solid protostele is correlated either with medullation (as in *Psilotum*) or stellation (as in *Astroxyylon*), with the result that the xylem-parenchyma ratio remains more or less constant. The same holds true in a general way for these forms with secondary wood. The primary body of *Palaeopitys* is the smallest and is a solid cylindrical protostele. In the other three the primary body is larger and is either more or less stellate as in *Tetrastichia* and *Aneurophyton*, or mixed as in *Sphenoxyylon*. It seems evident that the stellate protoxylem (actinostele) had its origin from the protostele at a very early date and that both types independently gave rise to secondary growth.

TYPE II

The woods grouped under Type II constitute a rather uniform assemblage, at least as far as the structure of the secondary wood is concerned. The segregation of *Lyginopteris* from the other members is based on a difference in degree—the

greatly dilated rays as they pass outward seem to be more generally characteristic of this plant than those placed under the sub-type B.

The series of three drawings in pl. 14, fig. 42, represents portions (as the rays of *Lyginopteris* are exceedingly high, often exceeding 2 cm., it is not possible to show complete rays without making an unduly large plate) of a few rays of *Lyginopteris*. At *a* the rays are shown as they appear close to the pith, at *c* as they appear at the outer border of the secondary xylem, while at *b* they are shown midway between. The total radial distance from *a* to *c* was 2.7 mm. The rays do not often attain greater tangential dimensions than those shown in *c*, and it may be noted even here, in the lower left-hand corner of the figure, that the ray is being split at two different points.

The vertical fusion of rays as they pass toward the outside is not an uncommon feature. In fig. 42*c*, the ray at the right now extending the full length of the figure has resulted from the fusion of two separate vertically aligned rays in *a* and *b*.

The question of the phylogenetic origin of the multiseriate ray is one that has long been disputed by anatomists, evidence having been brought forward by Jeffrey and his students in support of an origin from the aggregation of numerous uniserial rays, and by Bailey and others in support of the widening of a uniserial ray. In 1914 Bailey and Sinnott wrote:

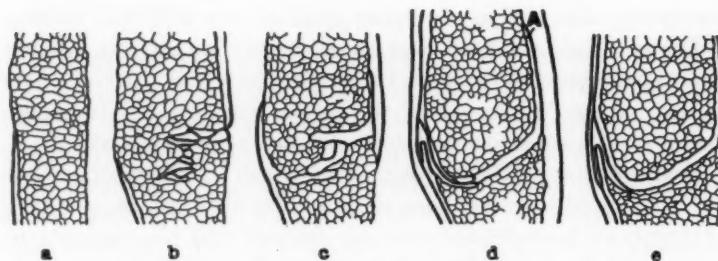
"Multiseriate rays of varying width are well developed in the majority of arborescent or shrubby dicotyledons and may be traced through the Tertiary to the Middle Cretaceous . . . The investigation of the structure and development of rays in the various families of the dicotyledons reveals much evidence that the multiseriate rays originated by the gradual widening of primitive uniserial rays."

In view of the evidence presented by both Schools it seems quite likely that the multiseriate rays have had a dual origin. That they were formed ontogenetically in *Lyginopteris* by the dilation of uni- or biserial rays is well shown in fig. 42 but the bearing that this may have on the origin of homologous structures in more recent seed plants is open to question.

Although the tracheid-ray ratio varies considerably in this

plant these greatly dilated rays are general in occurrence and, although widest when in association with leaf traces, they are by no means confined to this region. In close proximity to the leaf traces the rays, as is usually the case, lose their characteristic shape.

Mechanics of ray division.—It has been possible in two of the pteridosperms to trace individual rays closely enough to determine the manner in which they divide. It was found that in *Cycadoxylon robustum* the actual mechanics of ray division follows essentially the same process as shown for *Cola togoensis* Engler & Kräuse by Miss Chattaway ('37). A single tracheid initial cuts diagonally across the ray, apparently in-



Text-fig. 1. Ray division in *Lyginopteris oldhamia*. Explanation in the text.

creasing in length by sliding growth. The unique anastomosing nature of the tracheids and rays in this wood will be taken up below.

In *Lyginopteris* the case is somewhat different, for the rays do not simply divide by the increasing length of a single tracheid initial. Blocks were selected in which the secondary wood was especially well preserved and a series of tangential sections was prepared by the cellulose-pull technique. Although transverse ground sections of *Lyginopteris* often present remarkably fine cellular details the delicate ray tissue is rarely sufficiently well preserved to produce a uniform series of tangential pulls. Of four especially well-preserved blocks treated in this way one proved to be somewhat superior to the rest (text-fig. 1). Of sixteen sections taken through a radial dis-

tance of 1 mm. those shown in the text-figure have been selected to show the mode of ray division. At *a* the ray may be observed prior to any indication of division; at *b* it has increased its tangential dimensions considerably and ten of the ray cells laid down by the cambial initials have become lignified, their walls being composed of bordered pits as in normal tracheids. Although some of these lignified cells are no larger than the ray-parenchyma cells certain others are distinctly elongated. In *c* the number of lignified cells is smaller but those remaining are considerably larger and the ray has been almost completely dissected.

This increase in size of the lignified ray cells, or "ray tracheids," is apparently due to increase in size of certain cambial initials with resultant crowding out of the others. This increase merges imperceptibly into typical sliding growth as the later-formed lignified cells assume a more distinctly tracheidal shape. If the cell indicated at *A*, text-fig. 1*d* be compared with the corresponding ones in *c* and *e* respectively this becomes apparent; in the latter figure the cell formed from the same initial had so elongated that the end could not conveniently be included in the figure. The resultant U-shaped tracheids are not of uncommon occurrence, and when in association with leaf traces they may assume much more bizarre forms.

Although the division of the rays is primarily due to increase in size and sliding growth of certain initials there remains the possibility of the occasional fusion of the initials themselves.

These lignified cells may occur isolated in the rays unassociated with any later divisions. That is, an initial may lay down a ray cell which becomes lignified while the succeeding cell will remain a normal ray-parenchyma cell. New rays may be formed either by this division of one into two more or less equal parts or by a fragmentation process whereby a small arc-shaped portion of the ray is segmented off followed by a gradual dilation of the newly formed rays as shown in fig. 42.

Williamson and Scott ('96) noted that in *Lyginopteris*, "Ad-

ditional secondary rays appear *de novo* in the later formed layers, as secondary growth proceeds." . . . Their deduction was apparently based on transverse sections in which it is very difficult to ascertain positively the mode of origin of new rays. It is apparent that serial tangential sections present a much more positive means of determining ray origin, and while new rays may arise *de novo* the mode of secondary ray origin as described above is the only one that has been observed in the present investigation.

In subtype B the rays are for the most part very narrow, with nearly parallel sides, and of great height, being as high as 2 cm. or more in *Medullosa Noei* (fig. 41). In *Sutcliffia insignis* Scott (fig. 38) the rays are as high or higher. In slide 71 (0.73), University College Collection (London), three rays were measured having heights of 13.6, 17.6, and 14.0 mm., respectively; a fourth measured nearly 25.0 mm. These figures do not represent extremes but cracks or spots where the preservation is poor prevents the measurement of many rays throughout their entire height.

In *Calamopitys* the rays are very tall, quite uniform in their tangential dimensions, but somewhat broader than the other members of this subgroup (fig. 28).

Tangential sections through the xylem of the large outer steles ("snakerings") of *Medullosa Leuckarti* have been prepared by Mr. Hemingway.⁹ Although the cellular details are not well preserved the general shape of the rays is clearly defined. They are very narrow, most of them probably not more than two cells wide and well over a centimeter high. They are indeed quite similar to the rays of the Medullosae of the *anglica* section (Schopf, '39), such as *M. anglica* and *M. Noei*. That this similarity should exist is not surprising for other than being somewhat larger, the general stelar anatomy of *M. Leuckarti* is not vastly different from *M. anglica*. The latter does of course lack the star-rings but this is perhaps not a point of great distinction since there is one present in *M. centrofilis* which Seward ('17) described as forming "a connect-

⁹Slides Nos. 1060, 1061, in the Botany School, Cambridge.

ing link with certain continental Medullosae." The structure of the rays tends to confirm Schopf's tentative inclusion of this species in his subgenus *Anglorota* (Schopf, '39).

Megaloxyton presents somewhat of an exception in that its ray structure is more or less intermediate between subtype II B and Type III. The rays (fig. 40) do not reach the extreme height characteristic of II and smaller rays are more abundant. The larger rays tend to be fusiform although more elongate vertically and not as broad as the rays of Type III.

TYPE III

The members of Type III possess rays varying from elongate-fusiform to cylindrical. In general they are quite distinct from the high, narrow, parallel-sided rays of the preceding group. The pitting of the tracheids is likewise somewhat different as will be pointed out later. In view of the more or less transitional *Megaloxyton* I am inclined to believe that the members of this group may not be fundamentally different from those of Type II but rather represent an end line of development from the latter, typified in the extreme by the bizarre *Cycadoxylon anomalum*.

Cycadoxylon anomalum.—This remarkable wood has been mentioned a number of times in the literature since its original description by Williamson in 1878. However, inasmuch as certain details of its structure have never been adequately figured and certain questions have arisen with regards to possible identity with *Cycadoxylon robustum* (Seward, 1897) a re-investigation was undertaken. Two fragments of the original block were located in the Hunterian Museum, Glasgow, one of which has been utilized for the study of the rays. A second and somewhat larger fragment is preserved in the Williamson Collection at the British Museum.

The fragment of secondary wood upon which the species is based was collected from the Lower Carboniferous of Arran. It is especially remarkable that such a highly specialized wood should be found in this low horizon, and some doubt has been cast by those familiar with the locality as to its actual derivation from these rocks.

Although originally described by Williamson under the name of *Lyginodendron anomalum* (Williamson, 1878) it became evident that there was no close affinity with *Lyginodendron* (*Lyginopteris*), and it was subsequently placed in Renault's genus *Cycadoxylon* by Williamson and Scott (1896). In his description of *Cycadoxylon robustum* Seward (1897) suggests a similarity between *C. anomalum* and that portion of *C. robustum* where the wood is disturbed by a leaf trace:

"The resemblance between *Lyginodendron robustum* and *Lyginodendron anomalum* as regards the structure of the wood and the form of the medullary rays, which is specially striking in the wood of the former species where the normal form of the rays is modified by the bending of the tracheids to a leaf-trace bundle, points to the possibility of the two forms being closely allied to one another."

In order to check the constancy of the ray structure of *C. anomalum* a small block was studied first by means of serial tangential pulls through a radial distance of approximately 2 mm. When it was found that there was almost no change in the structure of the rays through this distance the block was ground more rapidly and photographs made directly from the etched surface by means of reflected light.¹⁰ This was carried on through a radial distance of approximately 1.5 cm. where there was very little change in the ray structure. It is certain then that there is no close similarity between this constant tracheid-ray relationship and the very irregularly contorted rays in *C. robustum* where they are associated with the leaf traces. A careful comparison of the slides of both species in the Williamson, Scott, and Cambridge Botany School collections, combined with the constant ray structure of *C. anomalum* as shown above, leaves no doubt as to the specific distinction of the two. In fact, it is probable that the distinction is a generic one.

The pitting of the radial walls of the tracheids shows considerable variation from the closely compacted reticulate pitting figured by Williamson (1878). Although the crowded

¹⁰ Very satisfactory photographs were obtained when the silicified block was roughly ground down with #150 carborundum, smoothed with #500, etched for five minutes in 25 per cent hydrofluoric acid, dried, and photographed with reflected light.

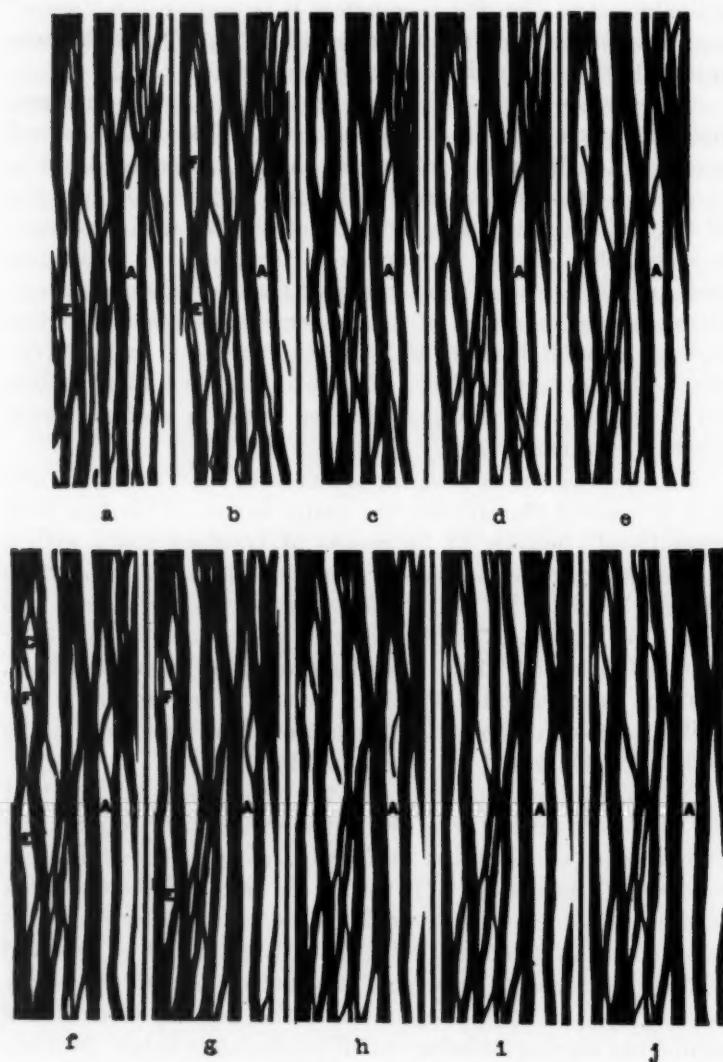
reticulate type (fig. 26) is common it is more often "loose" with the pits irregularly arranged (figs. 25, 27) and in some tracheids they are quite distantly scattered (fig. 24).

Cycadoxylon robustum.—This wood was treated in essentially the same manner as *Lyginopteris*. Although quite well preserved, sufficiently satisfactory preparations could not be obtained by the cellulose-pull technique. A preliminary series of the latter through about 1 mm. of the wood did indicate, however, that ground sections could be prepared sufficiently close together to show the significant features of the anatomy. Consequently, a series of 14 tangential sections extending through a radial distance of 2.5 cm. was prepared by Mr. Hemingway from fragment No. 3 of the original block (V4280 British Museum), the average distance between sections being slightly less than 2 mm.

A region was then selected which was representative and well preserved throughout the entire series. This has been reproduced (text-fig. 2) by means of tracings made with a photomicrographic projector. The drawings correspond to slides 1, 3, 5, 6, 7, 10, 11, 12, and 14, respectively.¹¹ Those sections (Nos. 2, 4, 8, 13) which show no appreciable change over the ones preceding them have been omitted from the series. Text-fig. 2a represents the section nearest (2 cm. from) the pith while *j* represents the outermost section. The tracheidal tissue is shown in black and the rays in white.

The most interesting feature of the wood lies in the fact that the new rays cut off from the older ones do not retain their individuality and increase uniformly in size as shown in *Cola togoensis* (Chattaway, '37); rather the rays and the tracheids form an anastomosing network. In order to understand this relationship an individual ray, *A* in text-fig. 2a, will be followed through the series of drawings. In *a* a small portion of the ray is being split off at the top and in *b* this is completed; in *e* a second ray segment is being cut off immediately below the first; in *f* this second division is complete, there being now three distinct rays; in the next figure, *g*, the first of the newly formed

¹¹Preserved in the British Museum (Natural History), London.



Text-fig. 2. *Cycadoxylon robustum*. Series of ray tracings showing the anastomosing nature of the ray-tracheid tissue.

rays has again fused with the "parent" ray, in *h* the second segment follows and is completely fused in *i*, resulting in a single individual ray again.

While these changes have been progressing in the upper portion of the ray A it will be noticed that another division has taken place in *b*, a little above the lower extremity of that portion of the ray shown in the figure; in *d* two small rays are cut off, while in *c* all four have again fused.

As a second example the ray E in text-fig. 2a may be followed: this divides to form two equal rays (E and F) in *b*; F divides again (figs. *d* and *e*), producing the two rays F and C in *f*, while F and E fuse again in *g* and remain thus throughout the remainder of the series. Although the structure of any single ray may not remain constant for any great radial distance the general tracheid-ray relationship at any point throughout the secondary wood shows no appreciable variation.

Medullosa Solmsii.—There remains much to be known of the Permian Medullosas of Chemnitz, and it is more than likely that when further knowledge is forthcoming those plants included within the genus must be segregated into a number of different genera. In general, the rays of the Permian forms are lower and more fusiform than those of the English and American species.

The detailed anatomy of the remarkable *M. Solmsii* is but little known, and the structure of the rays has, to my knowledge, never been figured. Weber and Sterzel (1896) figured a tangential cut through the outer ring of meristoles in a specimen of the variety *typica* but it is not sufficiently clear to show the structural details.

Five tangential sections have been prepared from two different meristoles by Mr. Hemingway and two prepared from a third meristole by the author. These sections include both the "internal" and "external" portions of the secondary wood composing the meristoles.

This wood is frequently disturbed by the passage of leaf traces. In the vicinity of the traces the rays are, as is usually the case, broader, lower and less regular in shape. In that

portion of the wood farthest from the traces the rays are quite tall but with a considerable admixture of lower uni- and biserrate rays (fig. 46). The rays do not approach the great height found in Type II, although there is no great dissimilarity between them and the rays of *Megaloxylon* which, as previously noted, is more or less intermediate between Types II and III.

Medullosa gigas B.R.—Slides of this species have not been available for study. However, judging from Renault's ('93-'96) description and figures the rays are similar to those of *Cycadoxylon robustum*, clearly justifying its inclusion within this group.

TYPE IV

Those plants included under Type IV have uniformly small rays, only a few cells high and mostly uniserrate, in striking contrast to either Types II or III. The rays of *Bilignea resinosa* (fig. 43) are typical for the group.

Endoxylon zonatum (fig. 44) presents a unique and very striking character in the oblique nature of the horizontal walls of the ray cells. This does not occur in all the rays, as may be seen in the figure, but the majority possess it.

It has been pointed out that the Calamopityeae includes genera which diverge very widely in certain of their characters. The variation in the structure of the secondary wood between certain members of the group is evident if either figs. 43 or 44 be compared with fig. 28 (*Calamopitys annularis*). Scott described such wood as cordaitean and it seems likely that the natural affinities of the following members of the Calamopityeae lie closer to the cordaitean-coniferous complex than to the pteridosperms: *Eristophyton fasciculare*, *E. Beinerianum*, *Endoxylon zonatum*, *Bilignea resinosa*, *B. solida*.

THE TRACHEIDAL MORPHOLOGY OF THE PTERIDOSPERMS

a. *Pitting types*.—The type of pits found in the tracheids of the secondary wood of certain of the pteridosperms is strikingly distinctive. The pits are irregular in size and shape (figs.

50, 51, 52), angular due to their crowded nature, and not arranged in any regular order. This type is characteristic of the following genera: *Heterangium*, *Lyginopteris*, *Rhetinangium*, *Stenomyelon*, *Calamopitys*, and *Medullosa* (*anglica* section). In addition to these, *Palaeopitys* and *Tetrastrichia* may be assigned to this group, and also *Aneurophyton* judging from Kräusel and Weyland's description ('29): "die Wände der vierseitigen oder polygonalen Zellen sind in ihrer ganzen Ausdehnung mit netsformig angeordneten Tupfeln bedeckt." Although the pitting occasionally may be typically alternate (fig. 53) it is comparatively rare.

It should be noted, furthermore, that the pits of the metaxylem tracheids of these same woods are universally of this reticulate bordered type, differing from those of the secondary wood only in their often more irregular size and shape (fig. 49). Certain uncatalogued slides of *Stenomyelon tuedianum* Kidston in the Scott Collection show particularly well the rapid transition from scalariform tracheids in the protoxylem to reticulate in the metaxylem (figs. 45, 52, 53).

The great geological age of these plants, the generally primitive nature of the primary body, and this rapid transition, all indicate that this reticulate-bordered pitting is palingenetically the primitive type for the metaxylem and the secondary tracheids of this group; there is no indication in any of the genera from the simplest, such as *Palaeopitys* and *Tetrastrichia*, to the more advanced members, such as *Lyginopteris*, that in the secondary wood this type of pitting was ever derived from an annular or scalariform type.

The close correlation of this reticulate-bordered pitting with the ray anatomy of the genera *Stenomyelon* to *Lyginopteris*, as shown in table II, is particularly significant. The range in structure of the primary body from a solid protostele through mixed protosteles to *Lyginopteris*, with a few scattered peripheral bundles, indicates clearly the comparative constancy of the secondary wood throughout the group.

The pits in the secondary wood of those members grouped under ray Types III and IV are either of the typical arauca-

rian-cordaitean type (figs. 54, 56) or are more or less scattered, round or oval. *Protopitys*, with its usually crowded elongate bordered pits, presents a very distinctive type (fig. 48). Such pits occur occasionally in *Mesoxylon multirame* but are not nearly as striking as in *Protopitys*. The figure of *Bilignea resinosa* (fig. 55) is more or less typical for that genus and *Eristophyton*. In *Cycadoxylon robustum* and *Megaloxylon Scotti*, although the pits are closely crowded, the arrangement is more regular (tending to vertical rows) than in those woods with the typical reticulate-bordered type. In *Cycadoxylon anomalum* the pits may be closely crowded (fig. 26) but they are generally more loosely arranged (figs. 24, 25, 27).

TABLE II
EXPLANATION IN TEXT

	Nature of primary body	Ray type	Pitting of radial walls of secondary xylem
<i>Tetrasporchia</i>	Solid protostele	I	Reticulate-bordered
<i>Aneurophyton</i>	Solid protostele	I	Reticulate-bordered
<i>Palaeopitys</i>	Solid protostele	I	Reticulate-bordered
<i>Stenomyelon</i>	Solid protostele with 3 narrow "rays" of parenchyma	II	Reticulate-bordered
<i>Heterangium</i>	Mixed protostele	II	Reticulate-bordered
<i>Ehetinangium</i>	Mixed protostele	II	Reticulate-bordered
<i>Medullosa</i> (<i>anglica</i> section)	Mixed protostele	II	Reticulate-bordered
<i>Calamopitys</i>	Mixed protostele but more highly medullated than the above three	II	Reticulate-bordered
<i>Lyginopteris</i>	Medullated with distinct scattered peripheral bundles	II	Reticulate-bordered

b. *Pitting in the tangential walls of the tracheids of the secondary wood.*—Judging from accounts in the literature one would conclude that tangential pitting in Paleozoic woods is of rare occurrence. A careful examination of many of the stems of Devonian and Carboniferous seed plants or supposed seed plants reveals a somewhat different story. Reasons will be presented below which seem to indicate that the tangential walls of the secondary wood of all primitive seed plants, or

rather the stock from which seed plants arose, were pitted in the same manner as the radial walls.

In 1935 D. E. Thomas listed the following plants in which tangential pitting was known to occur: *Pitys antiqua*, *Palaeopitys Milleri*, *Callixylon trilobatum*, *C. Newberryi*, *Volkelia refracta*, *Mesoxylo n multirame*, *Bilignea resinosa*, *Sphenoxylo n eupunctata*.

Considering first those plants enumerated under ray Type I it may be noted that *Tetrastichia bupatides*, *Palaeopitys Milleri*, and *Aneurophyton germanicum* have all been reported as having tangential pitting. I have been able to examine slides of the first two in the Kidston and Gordon Collections, and for the third, Kräusel and Weyland ('29) write: "Die Mehrzahl der Tracheiden gleicht aber auch hier deren des sekundären Holzes, d.h. die Wände der vierseitigen oder polygonalen Zellen sind in ihrer ganzen Ausdehnung mit netzförmig angeordneten Tüpfeln bedeckt, die in ein bis sechs Reihen stehen können." . . .

The tracheids of these three plants then are pitted alike on the tangential and radial walls. Although the tangential walls of *Sphenoxylo n eupunctata* are abundantly pitted, the pits are, as Thomas points out, in many cells scattered and not crowded as in the radial walls. This tendency to lose the tangential pits correlates interestingly enough with the more advanced nature of the primary cylinder of *Sphenoxylo n* with its highly medullated primary body.

In addition to the above, I have observed tangential pitting in the following: *Sutcliffia insignis*, slide 71(0.73) University College, London; *Medullosa anglica*, slide A.M.7 Binney Collection, Cambridge; *Heterangium tillaeoides*, slide 1621 Williamson Collection, British Museum (Natural History); *Heterangium (punctatum?)*, Renault Collection, Natural History Museum, Paris; *Stenomyelon tuedianum*, uncatalogued slide in the Scott Collection, British Museum; *Heterangium* sp., slide 91 Gordon Collection, King's College, London, and numerous slides in my own collection.

The most striking occurrence of tangential pitting is found

in the last-mentioned *Heterangium* from Burntisland. Prof. Gordon has kindly allowed me to examine his slides and has placed in my hands a block containing portions of two stems. The excellent preservation of the structure made possible the preparation of a fine series of cellulose pulls through the zone of secondary wood. The latter is quite narrow, being little more than 0.5 mm. wide, but the pitting is *uniform on the tangential walls throughout* as shown in fig. 31. These specimens of *Heterangium* are closely comparable with *H. Grievei*.

It is particularly significant that the most primitive woods possessing secondary xylem (*Tetrastichia*, *Palaeopitys*, and *Aneurophyton*) should be pitted alike on the tangential and radial walls, and that the somewhat more advanced forms (*Sphenoxyylon* and *Heterangium*) show a tendency to lose the tangential pitting. The above-noted specimens of *Heterangium* from Burntisland possess uniform pitting on the tangential walls, while in *H. tillaeoides* and *H. punctatum* the pits are scattered. In more highly specialized forms still, such as *Medullosa* and *Sutcliffia*, this character becomes relatively rare.

c. *Tracheid measurements*.—The great length of the tracheids of such pteridosperms as *Lyginopteris oldhamia* and *Medullosa anglica* has been noted by previous workers. Actual measurements have never been made, however, due to the difficulty of obtaining tangential longitudinal sections showing the entire length of the tracheids and the impossibility of obtaining complete serial sections with the older technique. It is surprising to note how few good tangential sections of the relatively common pteridosperms are available in the great English collections, a lack which may be attributed to the emphasis placed on the primary body.

The tracheids were measured by means of complete series of tangential cellulose pulls taken through the secondary wood. Particularly well-preserved tracheids were chosen and traced centripetally and centrifugally through successive pulls in order to check the length accurately.

The tracheid lengths given for *L. oldhamia* are based on two blocks containing exceptionally well-preserved secondary

wood. Although only approximately 25 tracheids were followed in their entirety, the results are representative since the variation in those measured was not great. The average length was found to be 5.8 mm., with a minimum and maximum of 5.1 and 6.7 mm., respectively.

The two species of *Medullosa*, *M. anglica* and *M. Noei*, have tracheids of remarkable length. The figures given in table III are based on only two complete measurements, the length being so great that it is difficult to find a complete cell. In the blocks from which the measurements of both species were obtained many tracheids were traced for well over 1.5 cm. with no termination, and it is almost certain that if figures could be based on more numerous complete cells the average length would be actually greater than that given.

In the following table figures for other gymnosperms are included for comparison, also for the dicotyledons taken from Bailey and Tupper ('18). These latter figures have been compounded from the numerous average measurements of the older wood (not the first annual ring) given for many genera and species included under the six groups.

TABLE III
TRACHEID LENGTHS (mm.)

	Average	Source of data
<i>Lyginopteris oldhamia</i>	5.8	Blocks supplied by J. R. Lomax and W. Hemingway
<i>Medullosa Noei</i>	24.0	Block in the Botany School Collections, Cambridge
<i>M. anglica</i>	17.5	Block supplied by J. R. Lomax
<i>Cycadoxylon robustum</i>	5.6	Block supplied by British Museum (Natural History)
Coniferae	3.6	Bailey & Tupper ('18), average of 35 gen. and 131 sp.
Cordaitales	5.	Bailey & Tupper ('18), average of 2 gen. and 2 sp.
Bennettitales	5.3	Bailey & Tupper ('18), average of 1 gen. and 2 sp.
Cycadales	6.8	Bailey & Tupper ('18), average of 1 gen. and 1 sp.
Ginkgoales	3.5	Bailey & Tupper ('18), average of 1 gen. and 1 sp.
Angiospermae-Dicotyledoneae	1.2	Bailey & Tupper ('18), average of 262 gen. and 276 sp.

The great length of the tracheids in *Lyginopteris* and particularly in *Medullosa* is not surprising when one considers their transverse dimensions. In *M. Noei* and *M. anglica* these cells may reach a diameter of 0.25 mm. and, although some few are as small as 40 μ or less, the average diameter is greater than that of any other seed plant that has come to my attention. It is interesting to compare the tracheid diameter of a few representative members of the Carboniferous pteridosperms with the vessels of the earliest known (Lower Cretaceous) dicotyledons:

TABLE IV
TRACHEID AND VESSEL DIAMETERS OF CERTAIN PTERIDOSPERMS AND LOWER CRETACEOUS DICOTYLEDONS RESPECTIVELY

Species	Average diameter in μ *	
	Vessel	Tracheid
<i>Lyginopteris oldhamia</i>		72.
<i>Medullosa anglica</i>		128.
<i>Rhetinangium Arberi</i>		45. - 85.
<i>Aptiana radiata</i> Stopes	28. - 40.	
<i>Woburnia porosa</i> Stopes	280. - 370.	
<i>Sabulia Scottii</i> Stopes	25. - 60.	
<i>Cantia arborescens</i> Stopes	30. - 50.	
<i>Hythia Elgari</i> Stopes	50. - 70.	

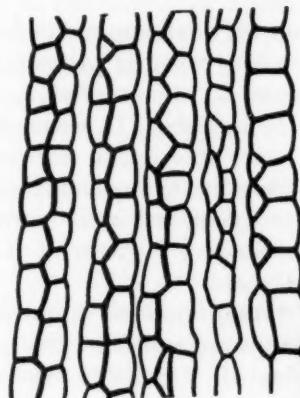
*Although the author has been able to study the slides of the five Lower Cretaceous dicotyledonous woods (*Aptiana*, *Woburnia*, *Sabulia*, *Cantia*, and *Hythia*) the figures are taken directly from Stopes ('12). The measurements for *M. anglica* are from slide 922, Andrews Coll.; for *L. oldhamia*, an average of about 600 cells, from slides 180, 183, Binney Coll., and 1147, 251, Scott Coll.

It is significant that the earliest known dicotyledonous woods described by Stopes ('12, '15) are, with the exception of *Woburnia porosa*, woods with vessels of exceptionally narrow diameter. The tracheids of the above pteridosperms not only equal but in some cases greatly surpass in diameter the vessels of these early angiosperms. The distinction, then, between diameters of tracheids and vessels in the higher plants vanishes when these fossils are taken into consideration.

The angular, irregular shape of the tracheids is particularly noticeable in *Medullosa* (*anglica* section), *Lyginopteris*,

and *Sutcliffia* (text-fig. 3). Tracheids of this shape are found in certain conifers and dicotyledons, and while perhaps of little significance their appearance is striking and has been commented upon by other paleobotanists.

It is significant that there is no trace to be found in the secondary wood of the pteridosperms of tracheids with scalariform pitting on their side or end walls such as has been described in certain families of angiosperms and considered to



Text-fig. 3. *Sutcliffia insignis*. Transverse section of secondary xylem (slide 5(040) Univ. College Coll., London). $\times 50$.

be an indication of a primitive nature. In view of the carefully compiled evidence obtained from living plants by such wood anatomists as Frost ('30, '31) and Kribs ('35) and since we have as yet no proof that the pteridosperms are ancestral to the dicotyledons, it seems best for the present to withhold further phylogenetic considerations in this respect.

LINES OF DEVELOPMENT IN THE PTERIDOSPERM COMPLEX

The discovery in recent years of new psilophytalean and supposed seed-plant stem remains, combined with a more detailed knowledge of the secondary wood of these early plants, materially facilitates a clearer understanding of the natural relationships of this Devonian-Carboniferous complex.

Since *Rhynia* presents the simplest known type of stele it will serve as a starting point in the present discussion. It is evident that two stelar types may have developed from such a protostele. With increase in size the primary body became either medullated or convoluted in order, supposedly, to maintain a more or less constant tracheid-parenchyma ratio. The fossil record clearly indicates that the actinostele arose very early, and like the protostele, acquired secondary wood at a very early date.

In a consideration of what appear to be primitive stelar types in which secondary wood is present, the genera under ray Type I (*Palaeopitys*, *Aneurophyton*, *Tetrastrichia*, and *Sphenoxyylon*) may be included. It seems reasonable to consider Prof. Harris' very interesting *Schizopodium* as an intermediate form between this group and the simple stelar types of *Rhynia* and *Asteroxylon*, but until more is known of the ontogeny of the "secondary" xylem of *Schizopodium* final judgment must be withheld.

A stele of the *Heterangium* type is not far removed from the above-mentioned group, and from this point a number of lines may have originated. First, with nearly complete medullation as in *Lyginopteris* and the development of extra-xylary rings as shown to occur in that genus the origin of the bizarre medullosas lies close at hand. Secondly, the cycadophytes may quite conceivably be derived from the *Heterangium*¹² type through such a form as *Megaloxylon*. Other than size there is not a great deal of difference between the primary body of the two. The peculiar aggregation of the tracheids to form a leaf trace in *Megaloxylon* is apparently due to the somewhat lower tracheid-parenchyma ratio of the primary body. The secondary wood is in certain respects intermediate between *Heterangium* and the cycadean type.

If it is ever possible to trace dicotyledonous ancestry to the

¹² The writer is quite aware of the danger of employing a few specific plants in building supposed lines of evolution. Names, however, are unavoidable in such a discussion, and it must be borne in mind that they are used only as a matter of convenience to convey types of structure represented.

Carboniferous it seems to me that the members of ray Type II present the most plausible group as far as potential plasticity is concerned. It is tempting to consider such phyletic implications with well-known pteridosperms of the *Lyginopteris* type but supporting facts are still notably lacking. As far as the stelar anatomy is concerned there is no sound basis for assuming such a line of development. Further discussion of the angiosperms with reference to the Paleozoic plants considered here could be only in the nature of a review or speculation. The subject has been adequately treated, from the standpoint of reproductive structures, by Dr. H. H. Thomas in his more recent papers.

SUMMARY

1. The distinguishing characteristics of the pteridosperms and their probable relationships to other groups are discussed generally.
2. The primary body of the stem and root of *Lyginopteris oldhamia* is considered in detail with reference to size variation, parenchyma-sclerenchyma relationship of the pith, and the nature of the primary xylem.
3. Medullary meristematic activity is discussed and a remarkable specimen described in which a complete medullary cylinder of supposedly secondary xylem is present.
4. It is pointed out that there are no gaps in the stelar variation of *L. oldhamia* sufficiently wide to permit segregation of varieties, whereas the foliage in organic connection or associated with the stems presents distinct specific segregation. This is explained partly on the basis of character phylogeny and partly on the physiological requirements of the primary body.
5. Evidence is summarized indicating the probable synonymy of *Calamopitys americana*, *C. saturni*, and *C. annularis*.
6. The primary body of certain other fossil and living plants is discussed in relation to "Size and Form" principles.
7. Four ray types are described for those plants generally included within the Pteridospermae.

8. The mechanics of ray division in *Cycadoxylon robustum* is shown to be essentially the same as Miss Chattaway described for *Cola togoensis*. In *Lyginopteris* the method is somewhat different and is described in detail.

9. *Cycadoxylon anomalum* is partially redescribed and is shown to possess a very constant ray structure and it is unquestionably distinct from *C. robustum*. The rays and tracheids are shown to anastomose.

10. Those woods included under Ray Types I and II, particularly the latter, possess a distinctive type of pitting, the pits being irregular in size and shape, closely crowded and irregularly (reticulately) arranged. The woods grouped under Ray Types III and IV possess either loosely arranged circular pits or the araucarian type.

11. It is pointed out that there is no evidence that the secondary tracheids of the pteridosperms ever possessed scalariform pitting. In the earliest known forms only well-developed bordered pitting is found.

12. It is shown that pitting in the tangential walls of the secondary tracheids is of much more common occurrence in these plants than is generally supposed. It is identical with the radial-wall pitting and occurs throughout the secondary wood in *Tetrastichia*, *Palaeopitys*, *Aneurophyton*, and certain specimens of *Heterangium*, and to a lesser extent in others.

13. The lengths of the secondary tracheids have been determined for *L. oldhamia* and *Medullosa Noei*.

14. As a whole it seems clear that the secondary wood offers more stable taxonomic characters than the primary wood, the latter being more readily affected by "Size and Form" factors.

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EXPLANATION OF PLATE

PLATE 5

Lyginopteris oldhamia. Transverse sections of stems, all $\times 7.5$.

- Fig. 1. Andrews Coll. 1140.
- Fig. 2. Manchester Coll. R838b.
- Fig. 3. Williamson Coll. 1885HH.



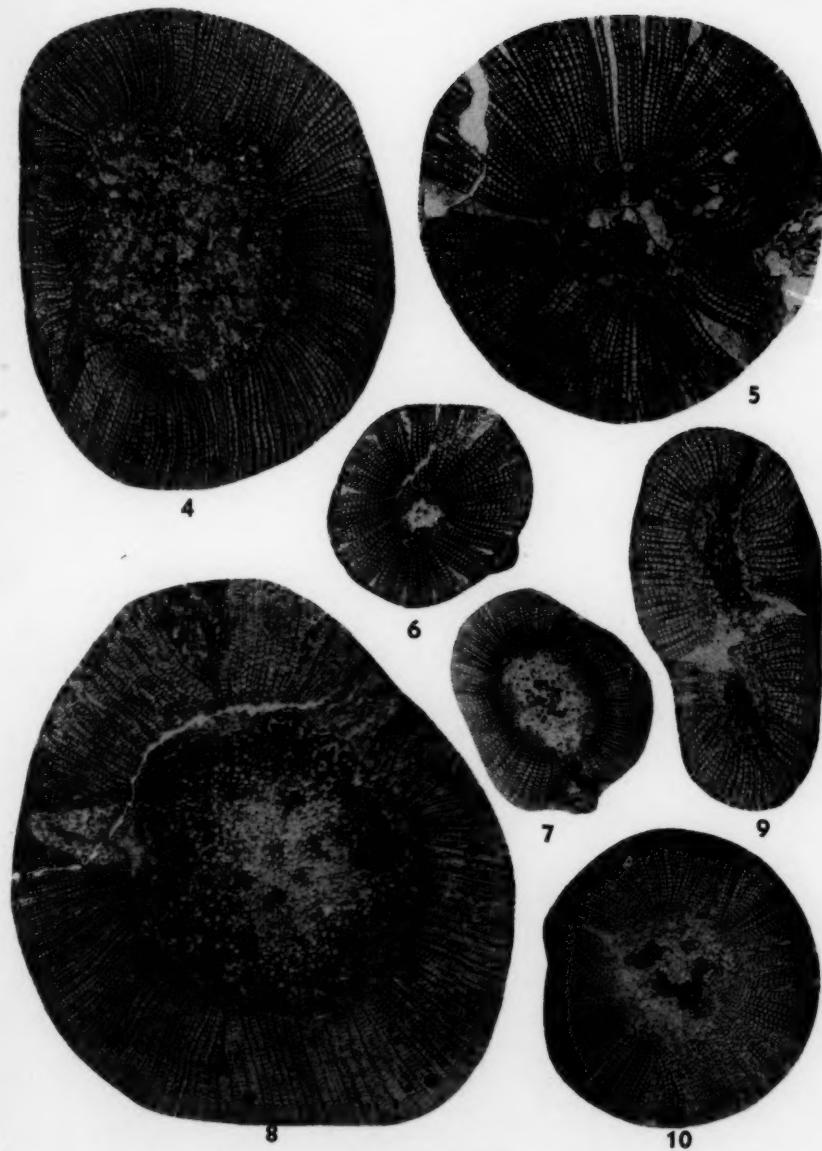
ANDREWS — PTERIDOSPERM ANATOMY

EXPLANATION OF PLATE

PLATE 6

Lyginopteris oldhamia. Transverse sections of stems, all $\times 7.5$.

- Fig. 4. Williamson Coll. 1116.
- Fig. 5. Binney Coll. 180. From the type specimen.
- Fig. 6. Andrews Coll. 611.
- Fig. 7. Scott Coll. 637.
- Fig. 8. Scott Coll. 251.
- Fig. 9. Cash (Manchester) Coll. Q10.
- Fig. 10. Williamson Coll. 1882.



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EXPLANATION OF PLATE

PLATE 7

Lyginopteris oldhamia.

Fig. 11. Central portion of fig. 14 more highly magnified. $\times 9$.

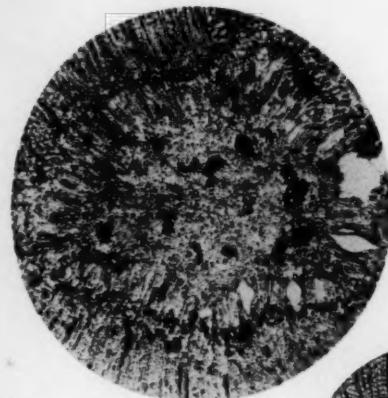
Fig. 12. Showing secondary centripetal xylem associated with a primary bundle. Manchester Coll. 1625. $\times 27$.

Fig. 13. Anomalous meristematic activity. Manchester Coll. R1059. $\times 8$.

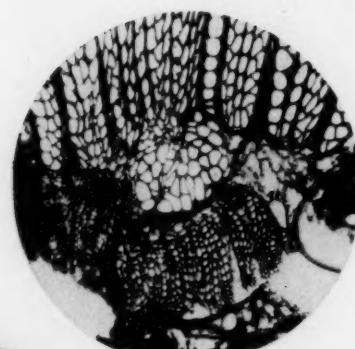
Fig. 14. Stem with complete ring of "centripetal" secondary xylem. Manchester Coll. R1060. $\times 7$.

Fig. 15. Same showing scattered nature of primary xylem adjacent to normal secondary xylem. $\times 26$.

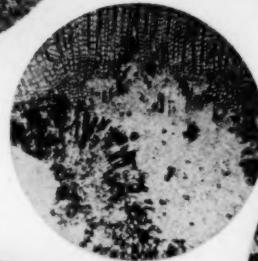
Fig. 16. Portion of fig. 14 shown at magnification of $\times 26$.



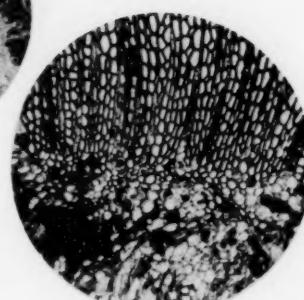
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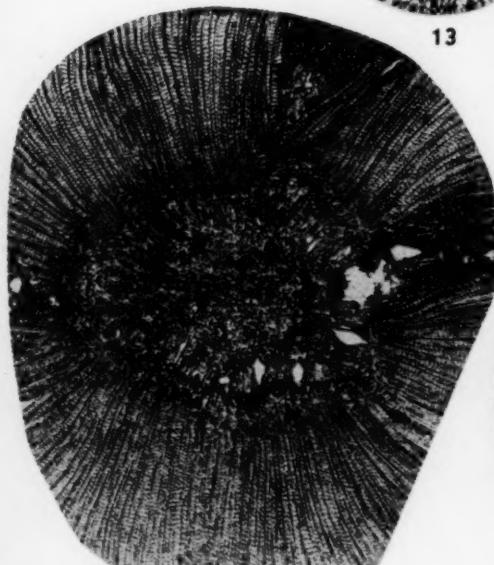
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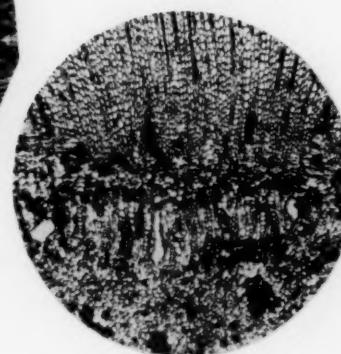
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EXPLANATION OF PLATE

PLATE 8

Fig. 17. *Lyginopteris oldhamia*. Manchester Coll. 1626. $\times 7.5$.

Fig. 18. *Calamopitys saturni*. Berlin Coll. 74. $\times 33$.

Fig. 19. *Lyginopteris oldhamia*. From an uncatalogued slide in the Scott Coll. (labeled 46) showing meristematic activity in the pith, with no signification. $\times 14$.

Lyginopteris oldhamia. Transverse sections of roots, all $\times 23$.

Fig. 20. Scott Coll. 647.

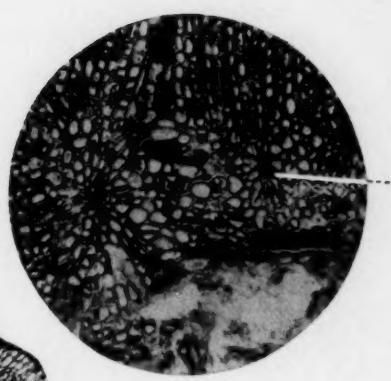
Fig. 21. Scott Coll. 647.

Fig. 22. Manchester Coll. 1060.

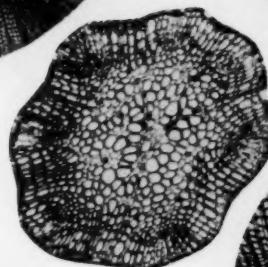
Fig. 23. Scott Coll. 645.



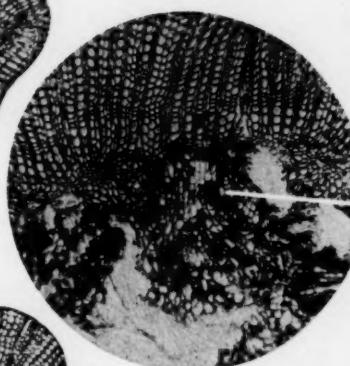
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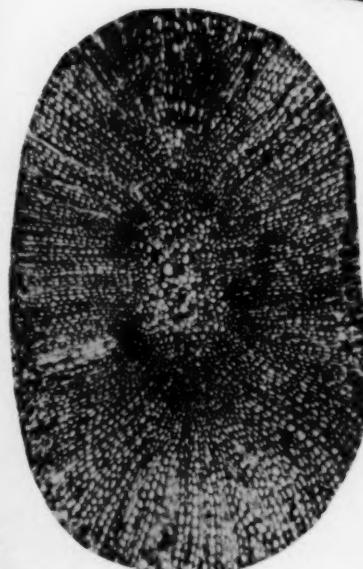
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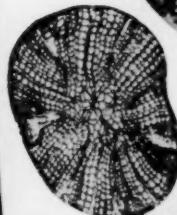
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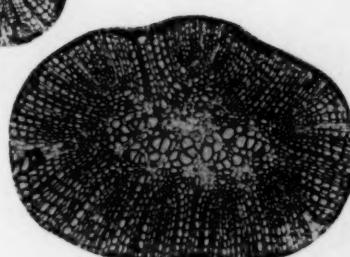
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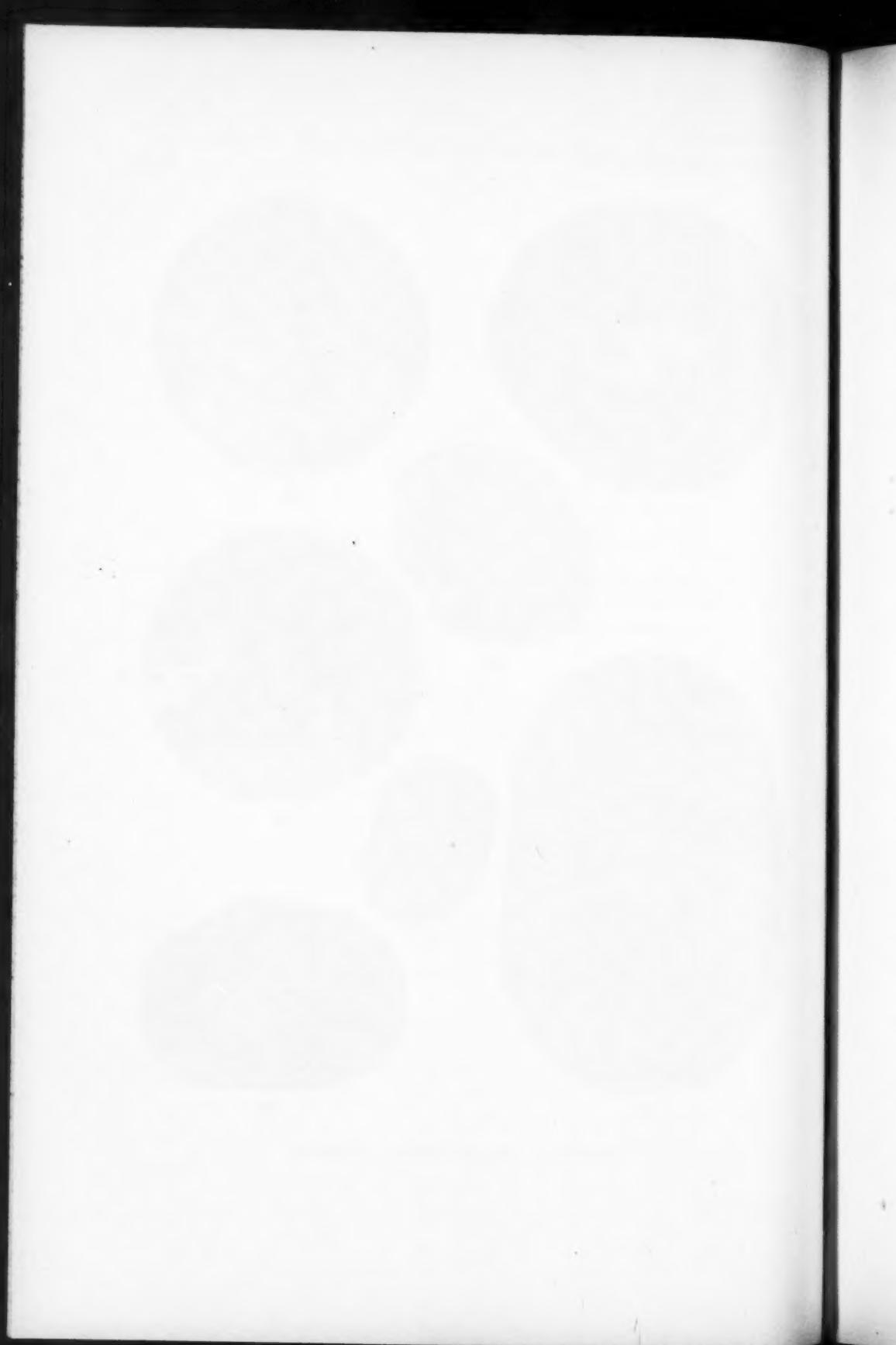


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EXPLANATION OF PLATE

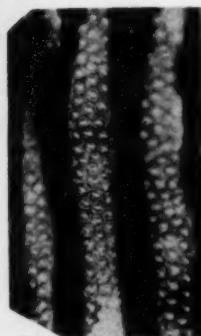
PLATE 9

Cycadoxylon anomalum. Pitting in the radial walls of the tracheids of the secondary xylem.

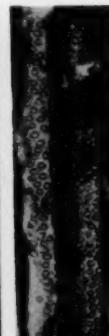
- Fig. 24. Scott Coll. 651. $\times 185$.
- Fig. 25. Scott Coll. 651. $\times 100$.
- Fig. 26. Scott Coll. 651. $\times 185$.
- Fig. 27. Scott Coll. 651. $\times 146$.

Calamopitys annularis.

- Fig. 28. Tangential section through the secondary xylem. Berlin Coll. 49. $\times 17$.
- Fig. 29. Showing portion of incomplete primary xylem ring. Berlin Coll. 97. $\times 11$.
- Fig. 30. Primary body. Berlin Coll. 74. $\times 14$.
- Fig. 31. *Heterangium* sp. Showing pitting in tangential walls of secondary tracheids. Gordon Coll. 91. $\times 55$.



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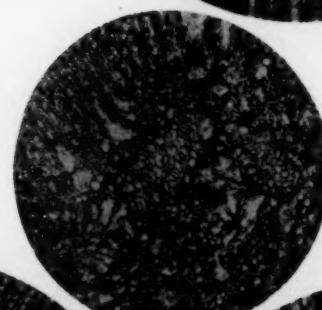
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EXPLANATION OF PLATE

PLATE 10

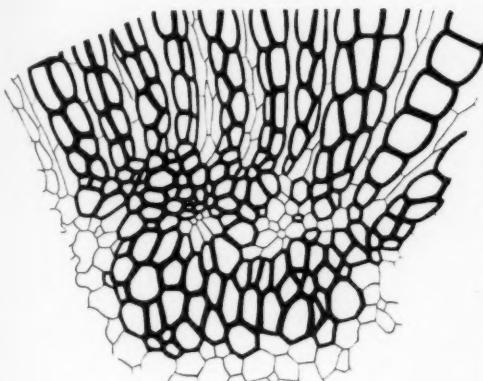
Lyginopteris oldhamia. Transverse sections showing variation in the nature of the primary xylem bundles, all $\times 65$.

Fig. 32. The normal type of bundle. Williamson Coll. 1882.

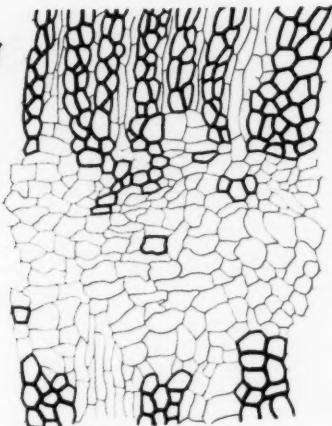
Fig. 33. From the specimen with complete ring of centripetal secondary xylem (fig. 14). The primary xylem is for the most part not aggregated into distinct bundles but consists of a few scattered cells.

Fig. 34. University College (London) Coll. M22V(19).

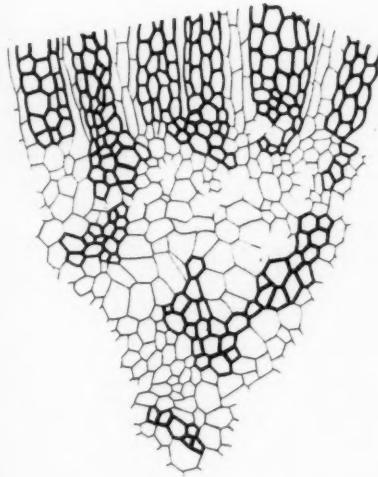
Fig. 35. Manchester Coll. 1626.



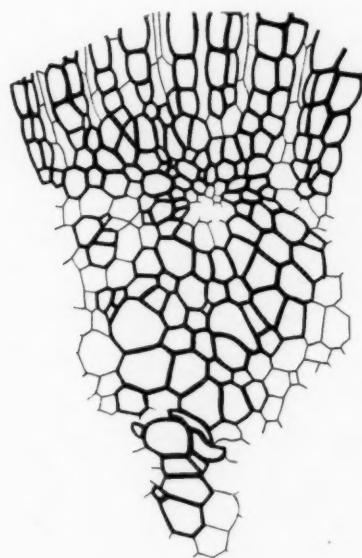
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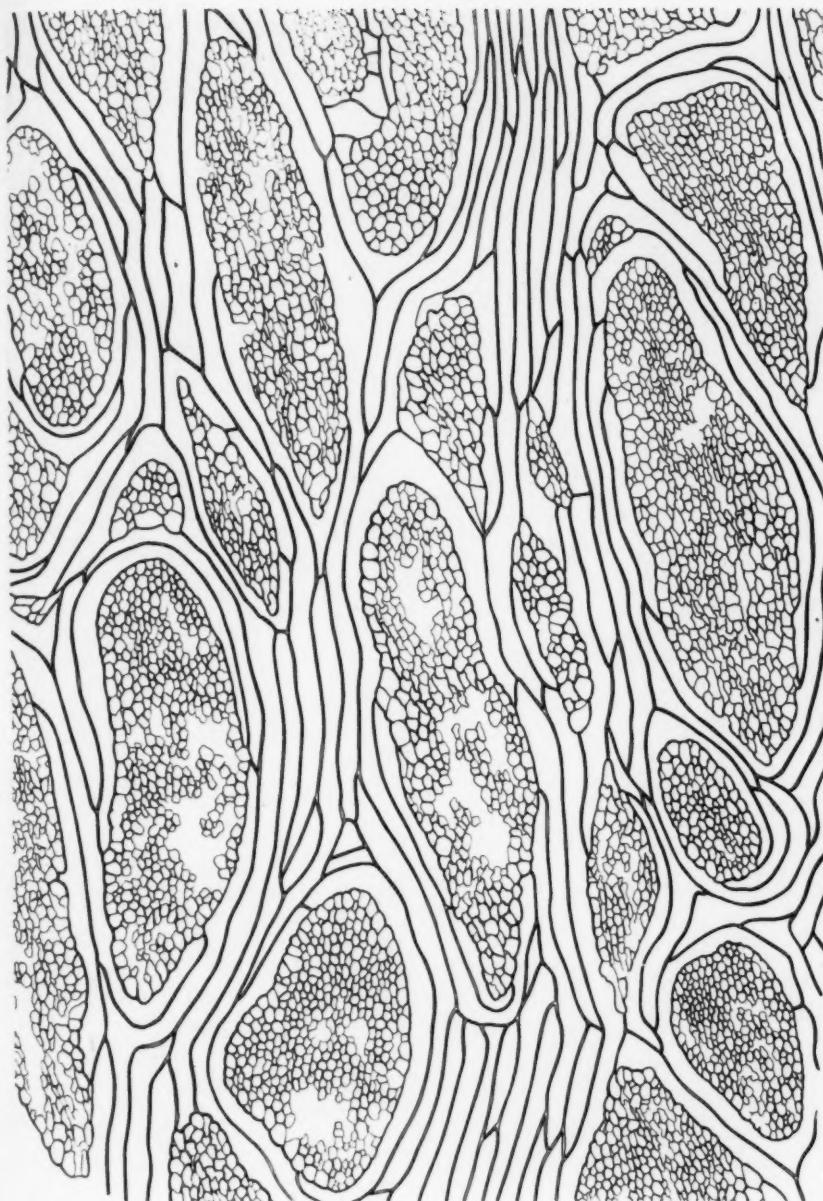
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EXPLANATION OF PLATE

PLATE 11

Fig. 36. *Cycadoxylon anomalum*. Tangential section through the secondary xylem. $\times 40$.

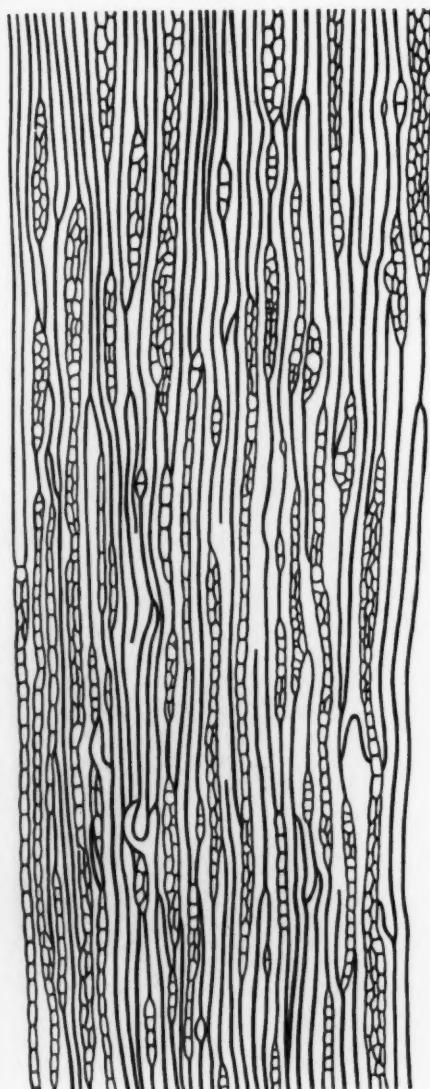


EXPLANATION OF PLATE

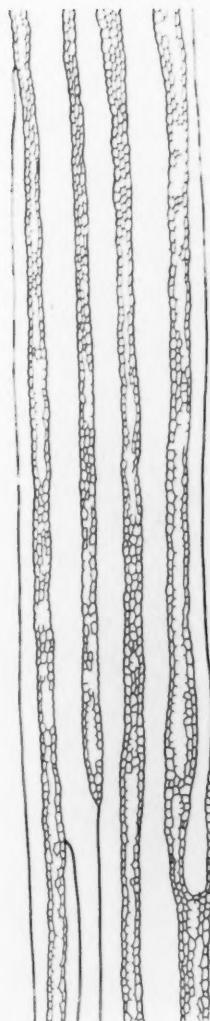
PLATE 12

Fig. 37. *Sphenoxyylon eupunctata*. Tangential section through secondary wood.
x 40.

Fig. 38. *Sutcliffea insignis*. Tangential section through secondary wood. x 40.



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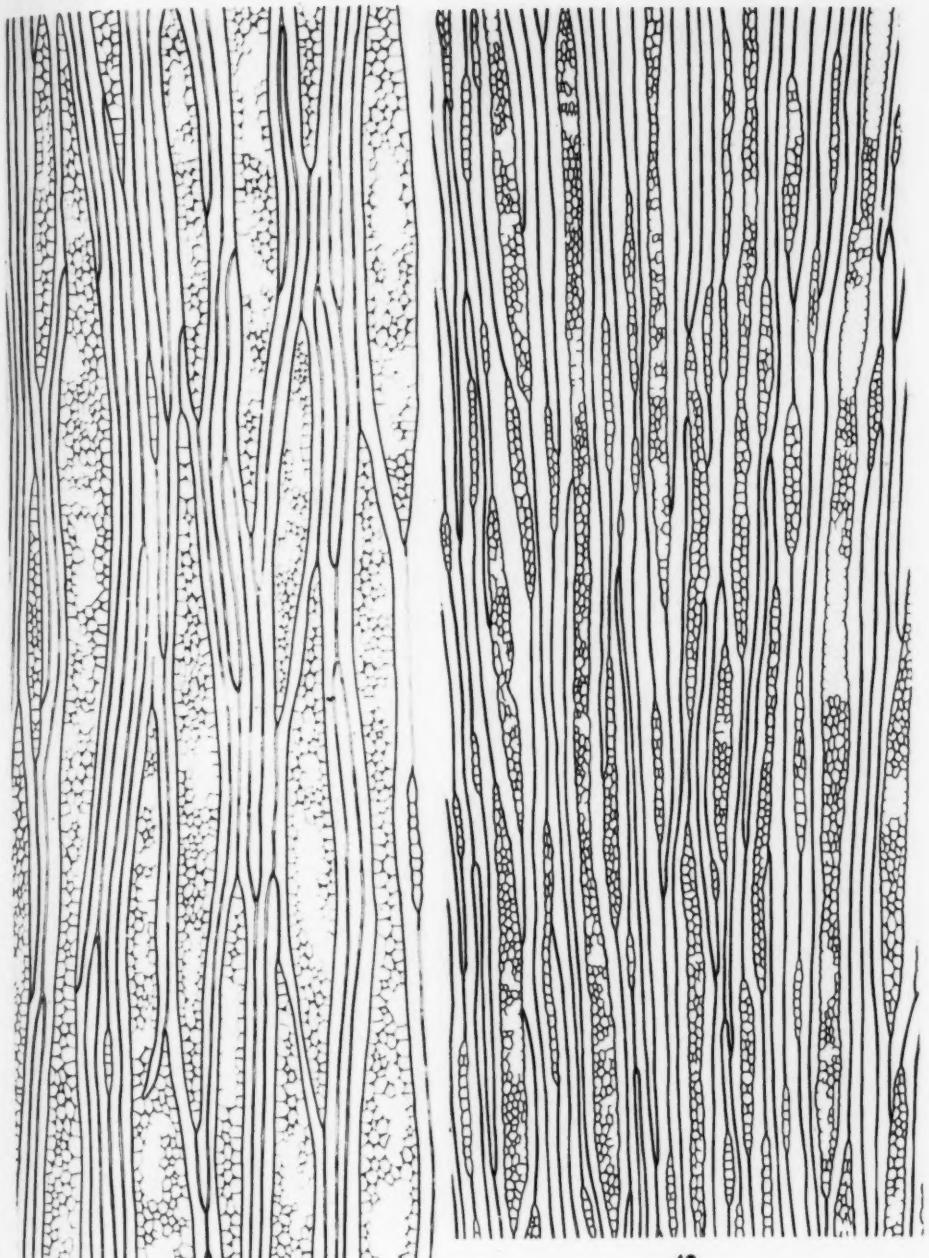


EXPLANATION OF PLATE

PLATE 13

Fig. 39. *Cycadoxylon robustum*. Tangential section through secondary xylem.
x 40.

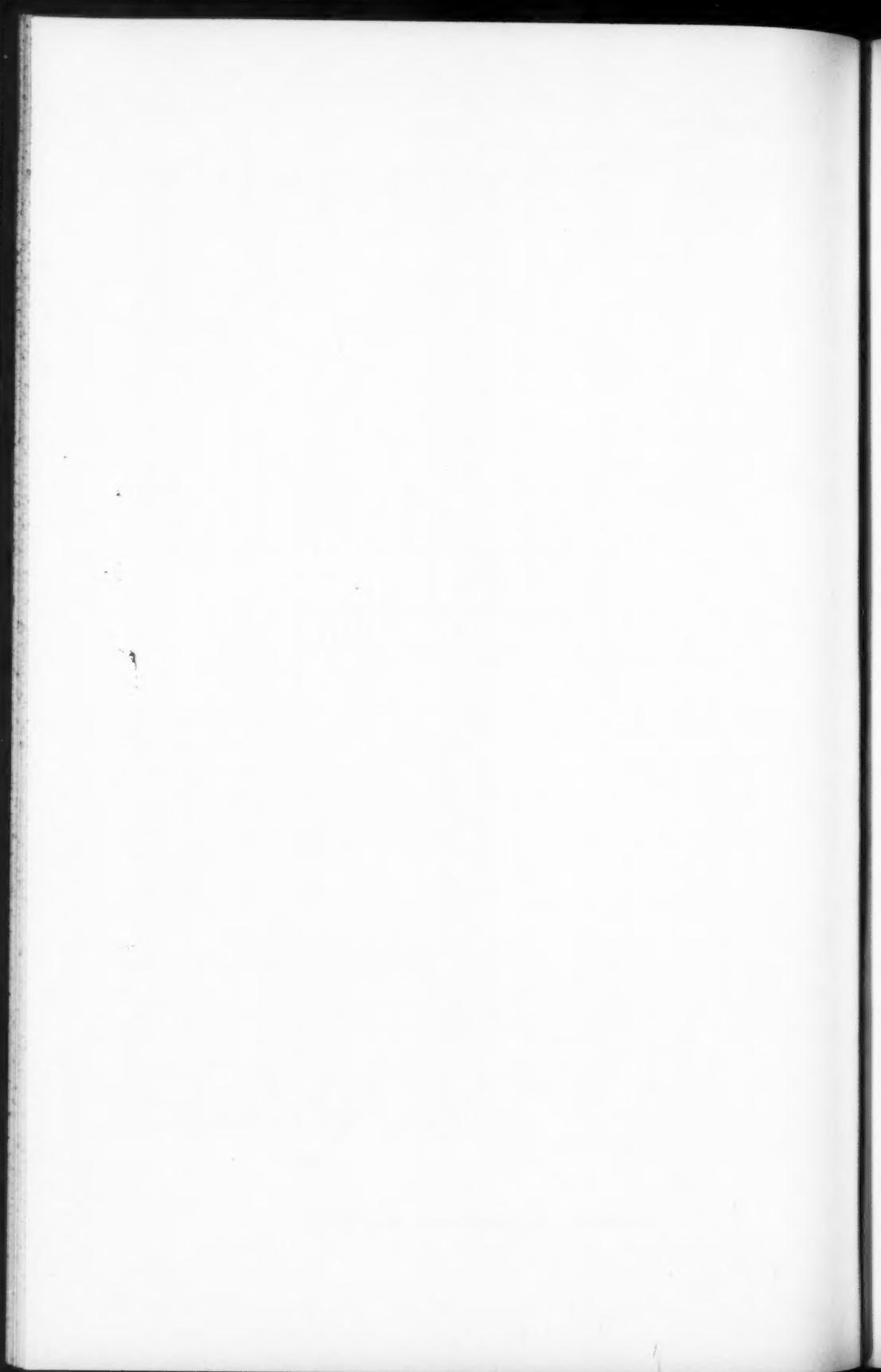
Fig. 40. *Megaloxylon Scotti*. Tangential section through secondary xylem.
x 40.



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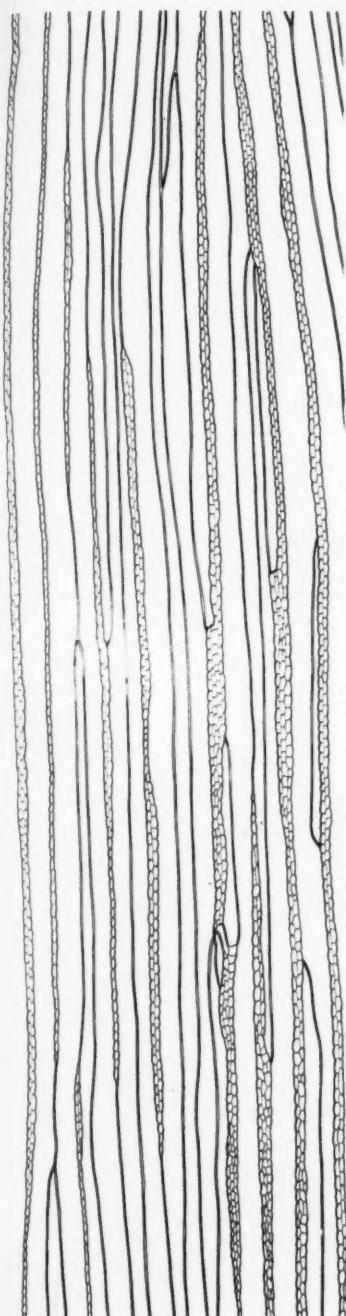


EXPLANATION OF PLATE

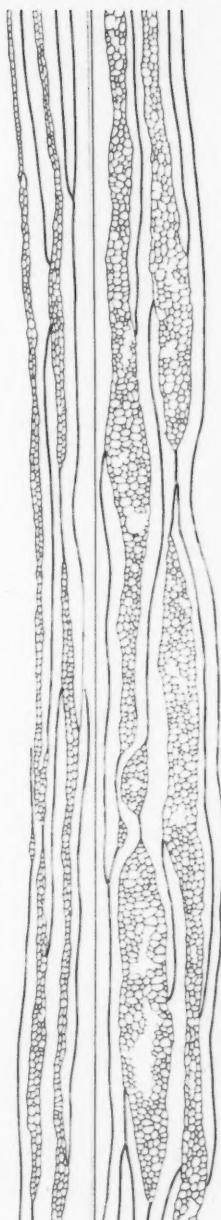
PLATE 14

Fig. 41. *Medullosa Noei*. $\times 40$.

Fig. 42. *Lyginopteris oldhamia*. Showing increase in size of two rays in passing from the pith towards the periphery of the secondary xylem; *a*, the rays bordering on the pith; *b*, the rays about half-way out; *c*, the rays near the outside limit of the secondary xylem. $\times 40$.



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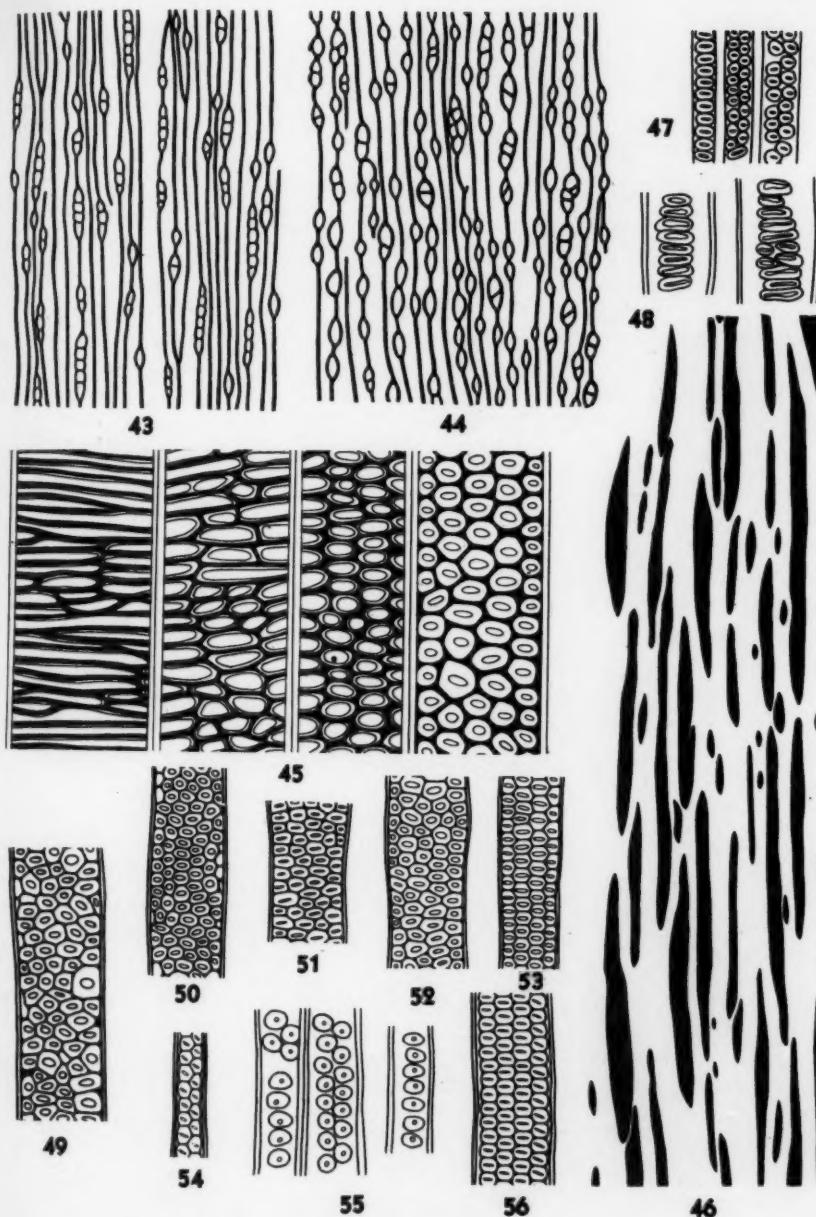
EXPLANATION OF PLATE

PLATE 15

Fig. 43. *Bilignea resinosa*. Tangential section through secondary wood. $\times 40$.
 Fig. 44. *Endoxylon sonatum*. Same as above.
 Fig. 45. *Stenomyelon tuedianum*. Longitudinal section through primary wood showing transition from protoxylem to metaxylem. $\times 300$.
 Fig. 46. *Medullosa Solmsii*. Tangential section through secondary wood. Rays in black. $\times 37$.

Pitting in the tracheids of certain woods included within the Pteridospermae.
 All figures of the radial walls of secondary tracheids, except 49, which is a metaxylem tracheid; figs. 49, 50, 51, 52, 53, traced from photographs; figs. 47, 48, 54, 55, 56, from camera-lucida drawings. All approximately $\times 170$.

Fig. 47. *Mesoxylo multirame*. (Scott Coll. 2360).
 Fig. 48. *Protopitys radicans*. (Kidston Coll. 3111).
 Fig. 49. *Rhetinangium Arberi*. (Gordon Coll. 1077).
 Fig. 50. *Rhetinangium Arberi*. (Gordon Coll. 936).
 Fig. 51. *Calamopitys annularis*. (Berlin Coll. 101.44).
 Fig. 52. *Stenomyelon tuedianum*. (From uncatalogued slide in the Scott Coll.).
 Fig. 53. Same as above.
 Fig. 54. *Dadoxylon* sp. (Scott Coll. 1508).
 Fig. 55. *Bilignea resinosa*. (Kidston Coll. 2742).
 Fig. 56. *Poroxylon Edwardsii*. (Scott Coll. 3336).



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